

INFLORESCENCE UNITS IN THE CYPERACEAE¹

LIENE TEIXEIRA EITEN²

ABSTRACT

A classification of ultimate inflorescence units in the Cyperaceae is proposed, establishing six groups. It is concluded that there is no evidence for considering: (1) the rachilla of the *Cyperus*-, *Scleria*- or *Rhynchospora*-type of spikelet to be sympodial; (2) nor the apparently simple flowers in the Cypereae, Scirpeae, and Rhynchosporeae to be pseudanthia; (3) nor the female flower in *Scleria* to be terminal; (4) nor the rachilla of the female flower-bearing spikelet in the Cariceae to be sympodial. Evidence is presented which throws doubt on the concept that *Scleria* is related to the *Diplacrum-Bequerelia* group of genera, and other evidence is presented which shows that the apparently terminal female flower in the Lagenocarpeae is really lateral.

One of the most important characteristics to be considered in dividing the Cyperaceae into subfamilies, tribes, and subtribes is the branching pattern of the ultimate branch orders of the inflorescence. As a result of 15 years' experience examining thousands of specimens, I present a new classification of these branching patterns. Six groups are distinguished which it is believed will account for all the genera of the family. Brazilian genera are mentioned as examples for each group; a few non-Brazilian genera (marked with asterisks) are also given when these are such that they extend the range of character variation which each group may contain.

Since the inflorescence units are extremely contracted and the internodes very slightly developed, the analysis of the branching patterns was based on the following morphological principles:

1. A stem arises from a stem in the axil of a leaf. In a few cases the subtending leaf may be absent. In the aerial part of the plant, the culm, culm branch, rachis, branches from the rachis, rachilla, and flower axis are successively higher branch orders of the stem, while bract, glume, glumella, scale, prophyll, utricle (perigynium), and some kinds of bristles are reductions and modifications of the leaf.

2. Leaves arise from stems.

3. A prophyll, recognized by its form and position, indicates the beginning of a new branch. This principle was always helpful when a prophyll was distal but contiguous to a bract. In this case the prophyll does not arise from the same axis as the bract but is really on a new, very short branch which itself arises in the axil of the bract.

4. When two glumes appear to arise at the same level, the one which is really more basal totally or partially surrounds the distal one.

5. The presence of a glumella or a bristle more internally placed than at least one stamen shows that the flowerlike structure in which it occurs is a pseudanthium and not a true flower.

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² Universidade de Brasília, Brasília, DF, Brazil.

6. In the angiosperms, flower parts always arise from a floral axis. Therefore, in the Cyperaceae, when a stamen appears to arise directly from the rachilla in the axil of a glume or glumella, it is really on an extremely short floral axis which arises from the rachilla in the axil of the glume or glumella.

In the following discussion of the six groups of ultimate inflorescence units, branching patterns are described, ultimate inflorescence units are defined, and, where necessary, spikelets are defined. The ultimate inflorescence unit may include axes of more than one branch order (not counting in this the floral axes of the lateral flowers, which make still another branch order). A spikelet, however, has only one branch order, the rachilla (besides the floral axes of the lateral flowers).

GROUP I

The axes of the inflorescence terminate in spikelets. The word "spikelet" in this paper is used in the strict sense, that is, a racemosely branched structure consisting of an axis (rachilla) of potentially indefinite growth bearing lateral, true flowers. Each flower arises in the axil of a glume (scalelike bract) which covers it. Besides flower-bearing glumes, empty glumes may be found at the base or at the apex of the rachilla (Fig. 1). A single spikelet may contain all bisexual flowers or both bisexual and male flowers. Very rarely, a taxon is dioecious such as *Cyperus schomburgkianus* Nees var. *leucanthus* (Schrad.) Kük. (Kükenthal, 1935–1936).

In Fig. 1, all the spikelets are shown arising from a rachis in the axil of a subtending bract and, in almost all the genera, the rachilla axis bears a basal prophyll. But in some spikelets of an inflorescence the subtending bract and prophyll may not be present. When a spikelet is lateral and sessile to an inflorescence branch, its subtending bract and prophyll are next to the spikelet and appear to be part of it. However, when the spikelet is terminal on an axis that bears other lateral spikelets, leaves, branches, etc., the subtending bract and prophyll occur at the base of that axis and so are separated from the terminal spikelet. For this reason, the subtending bract and prophyll, and the internode just below and just above the prophyll, are not considered here to be part of the spikelet even when they are next to it.

In *Eleocharis*, the spikelet is always separated from the prophyll of its axis by the length of the culm. In this genus, the leaf from whose axil a culm axis arises is one of the two tubular leaf sheaths of a previous culm. The new culm axis bears its prophyll at its base addorsed to the culm from which it sprang.

Group I consists of the tribes Scirpeae, Cypereae (when this is considered distinct from Scirpeae) and Rhynchosporae.

Examples of genera in the group are: *Cyperus* (sensu lato), *Remirea*, *Lipocarpha*, *Hemicarpha*, *Ascolepis*, *Androtrichum*, *Fimbristylis*, *Bulbostylis*, *Eleocharis* (including *Chamaegyne* and *Helonema*), *Websteria*, *Egleria*, *Scirpus*, *Fuirena*, *Rhynchospora*, *Dichromena*, *Pleurostachys*, and *Cladium*.

The inflorescence units of *Lipocarpha*, *Hemicarpha*, and *Ascolepis* merit a detailed discussion. They are related genera and have the same habit. Their inflorescences generally consist of 1–3 small ovoid heads each with a thick cen-

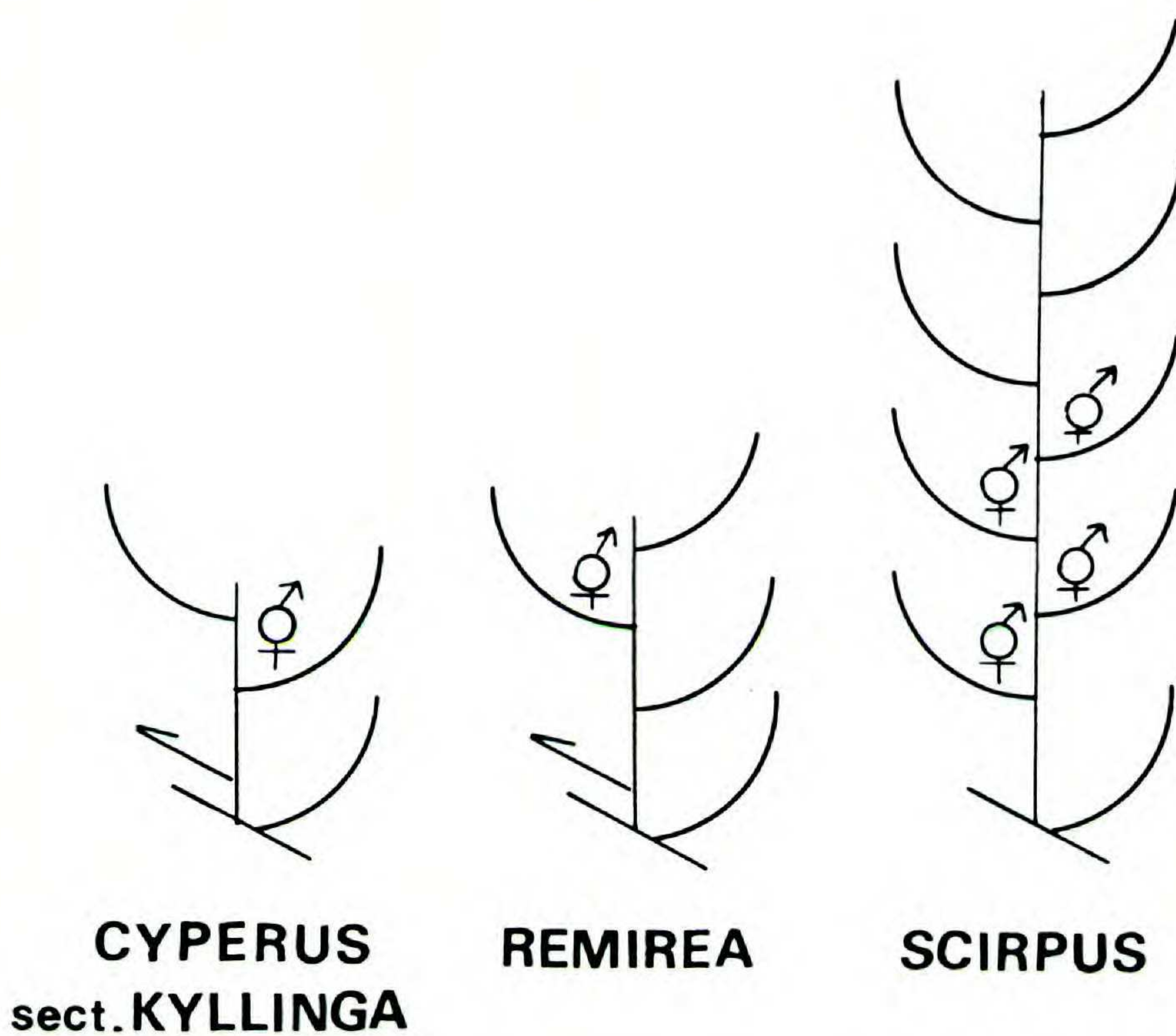
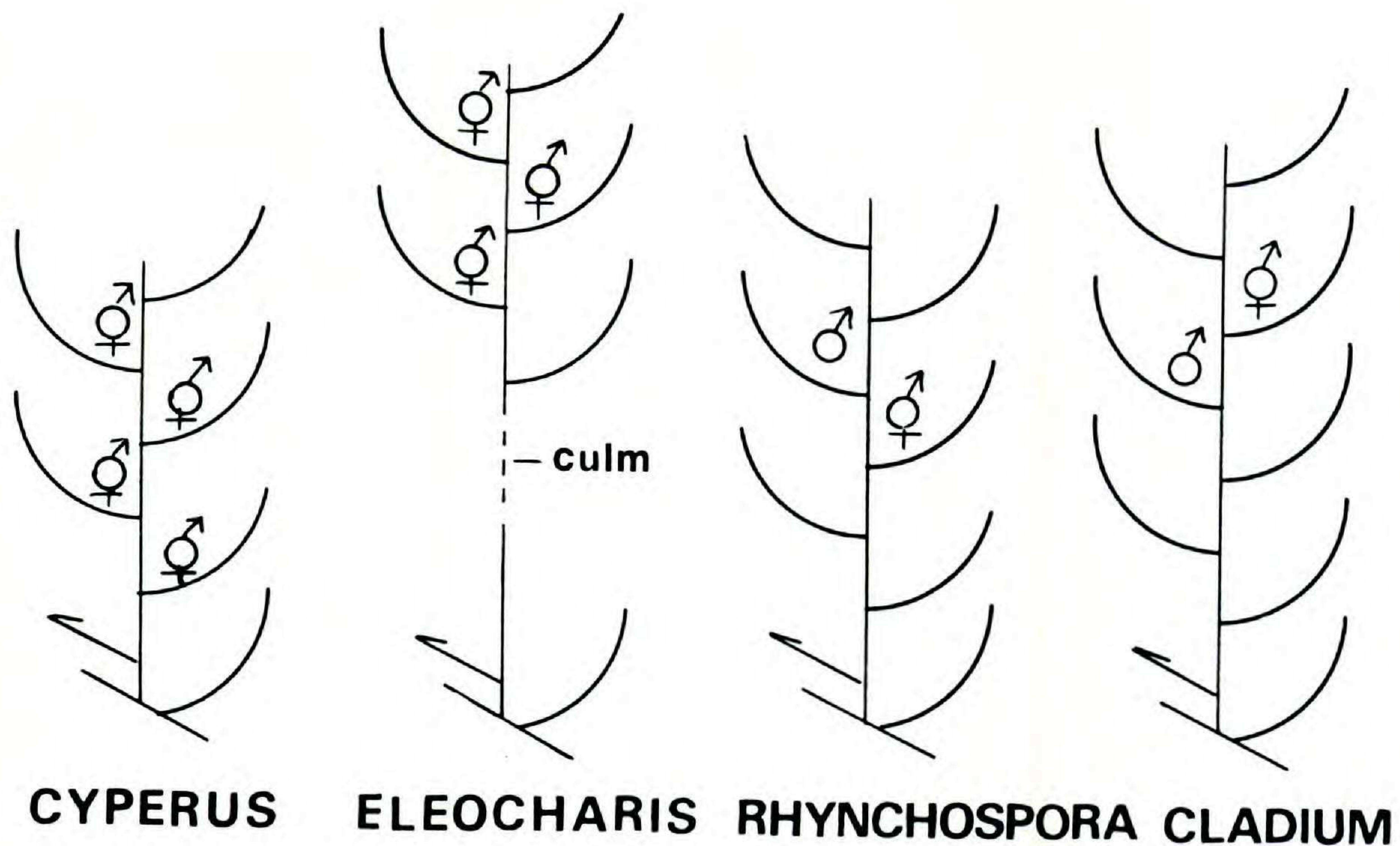


FIGURE 1. Spikelet branching patterns of genera of Group I. Each spikelet is shown with the prophyll (when it has one) of its rachilla axis, the bract from whose axil it arises, and a piece of the lower-order stem from which it branches off. The prophyll and bract are not considered to be part of the spikelet proper. Curved lines represent bracts and glumes, straight lines with hooks represent prophylls. In all diagrams of branching patterns in this paper, a stem axis arising in the axil of a bract is shown slightly separated from the bract symbol in order to show clearly its connection with the mother axis and not with the bract itself. Despite this separation, the branch axis and the subtending bract are considered to arise from the same node. A prophyll is always shown slightly separated from the origin of the axis which bears it in order to make clear from which axis it grows. In this case, the segment from the origin of the axis to the prophyll is a true internode, the subprophyllar internode.

tral rachis. A few species of *Ascolepis*, such as *A. brasiliensis* (Kunth) Bentham ex Clarke, have the same type of heads but other species of the genus, such as *A. capensis* Ridley, have heads with more or less flat compound receptacles as in many Compositae.

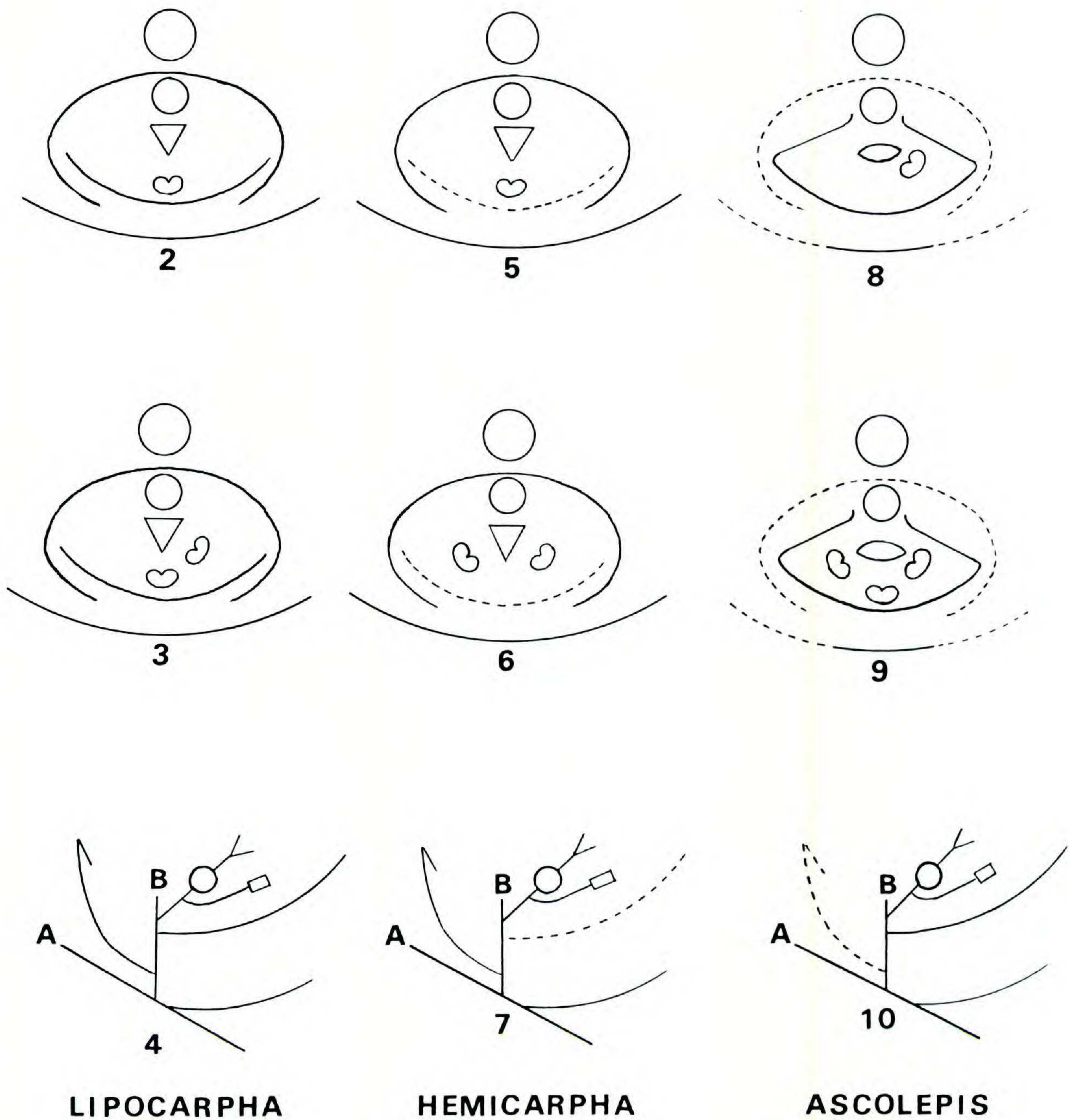
I consider the ultimate inflorescence units in these genera to consist of a bract from whose axil arises a rachilla bearing a single lateral flower. This interpretation is illustrated in Figs. 2–10.

Nees (1842) and Pax (1886) thought that *Ascolepis* (= *Platylepis*), *Hemicarpha*, and *Lipocarpha* are related to *Hypolytrum* and put these genera in the same tribe, Hypolytreae. Bentham (1883) placed *Ascolepis* with *Hypolytrum* in the tribe Hypolytreae, but also included in this tribe other genera which today are placed in the Mapanieae. To accept Bentham's grouping of these genera means that *Ascolepis* has the same basic structure as the genera of Mapanieae. In the present-day interpretation of the Mapanieae, the axis B bears an apparently terminal pistil which constitutes by itself a unisexual flower, and lateral stamens each constituting a male flower. But *Ascolepis*, as well as *Hemicarpha* and *Lipocarpha*, differs from the Mapanieae in the aspect of the plant and in the inflorescence. These three genera are very similar in habit to species of *Cyperus* sect. *Kyllinga*, such as *C. sesquiflorus* (Torrey) Mattf. & Kük., *C. densicaespitosus* Mattf. & Kük., and *C. brevicaulis* (Rottb.) Hassk. In herbaria one commonly finds specimens of *Ascolepis* and *Lipocarpha* determined as species of *Cyperus* sect. *Kyllinga*. Compare the drawings of *Lipocarpha*, *Ascolepis*, and *Hemicarpha* in Barros (1947: pars I, tab. XLVIII) and in Kükenthal (1935–1936: fig. 63E).

In *Cyperus* sect. *Kyllinga*, the spikelet often has only a single flower. The branching pattern in this case is given in Fig. 1. It is equal to that of *Lipocarpha* (Fig. 4) with the addition of an empty apical glume. The position of the stamens in *Lipocarpha*, *Hemicarpha*, and *Ascolepis* (Figs. 3, 6, 9) is such that the bisexual flower can be considered to be in the axil of the upper lamina (i.e., the glume) (Figs. 4, 7, 10). This is because in the Cyperaceae in general the stamens occur between the pistil and the glume which subtends the flower.

Another reason to exclude these three genera from the Mapanieae is the absence of the two basal, lateral, pilose-keeled laminas, characteristic of genera of this tribe. In *Lipocarpha*, *Hemicarpha*, and *Ascolepis*, on the contrary, the laminas are parallel to the glumiform bract which subtends the spikelet; these laminas are gently curved (not folded) in cross section and do not possess ciliate keels. For all these reasons, I consider the inflorescence units of these genera to be structures homologous to the one-flowered spikelets of *Cyperus* sect. *Kyllinga*.

In *Lipocarpha* (Fig. 4), beneath the covering bract, there are two thin laminas; the lower (outer) is considered a prophyll and the upper (inner) a glumella which subtends the bisexual flower. In *Hemicarpha* (Fig. 7) the upper lamina (glume) which subtends the flower disappeared in evolution so that the flower appears to be situated between the prophyll and the covering bract. In *Ascolepis* (Fig. 10), the prophyll disappeared and the upper lamina became transformed into the utricle which contains the flower. The sides of this lamina folded in and the margins fused, leaving a subapical orifice on the adaxial side.



LIPOCARPHA

HEMICARPHA

ASCOLEPIS

FIGURES 2-10. Floral diagrams and branching patterns of inflorescence units of *Lipocarpha*, *Hemicarpha*, and *Ascolepis*, genera of Group I. The triangle and fusiform symbol represent pistils; the reniform symbol, a stamen; the upper circle, the rachis (axis A in the branching patterns); the lower circle, the rachilla (axis B in the branching patterns). The curved lines represent subtending bract, prophyll and glume (the latter called "glumella" in *Lipocarpha* because it is small and thin); the broken-line curve represents parts which have supposedly disappeared in evolution. In the branching patterns, the hooked curves are prophylls; pistil and stamens are also shown.—2-3. Floral diagrams of *Lipocarpha* with 1 and 2 stamens.—4. Branching pattern of *Lipocarpha* inflorescence unit.—5-6. Floral diagrams of *Hemicarpha* with 1 and 2 stamens.—7. Branching pattern of *Hemicarpha* inflorescence unit.—8-9. Floral diagrams of *Ascolepis* with 1 and with 3 stamens. The glume is utriculiform with a subapical adaxial orifice.—10. Branching pattern of *Ascolepis* inflorescence unit. The spikelet proper, as defined in this paper, is, for these three genera, the upper part of the inflorescence unit, that is, the flower, its subtending lamina (glumella in *Lipocarpha*, utricle in *Ascolepis*, none in *Hemicarpha*), and that part of axis B from the insertion of this lamina, distally.

(The floral diagrams in Figs. 8–9 represent the utricle at the level of the orifice.) The utricle is larger and thicker than the homologous organ in the other two genera. Bentham (1883) and Pax (1886) thought that the utricle of *Ascolepis* was formed from two fused laminas. This is not probable because the vascular bundles of the utricle occur only in the abaxial side, so that it is more probable that the utricle is formed of only one lamina. In fact, in a specimen of *Ascolepis* from Zambia (*Richards 18918*,[K]) this lamina does not form a utricle; the margins at the base of the lamina turn in to form a narrow fold but remain free and distant from one another. In the upper portion of this lamina the margins do not even turn in. After having noted that the inflorescence pattern of these three genera is related to that of *Cyperus* sect. *Kyllinga*, I found that Palla (1905) had arrived at essentially the same conclusion.

From the discussion of Group I we see that the ultimate inflorescence unit in the group is of three types: (1) Spikelet (as defined in this paper) alone, when the prophyll and subtending bract of the rachilla axis are not close to the spikelet. (2) Spikelet with the prophyll (when this is present) and the subtending bract of its rachilla axis when these are close to the spikelet, the whole looking like a single unit. Most units found in Group I are of this type and include also the basal spikelets of *Eleocharis* (see discussion of these under *Chamaegyne* in the following paper, Eiten, 1976). (3) Spikelet with its basal associated scale when the latter is not separated from the spikelet by a developed shoot in the axil of this scale (see under *Helonema* in Eiten, 1976). This is found in the culm-tip spikelets of *Eleocharis* and its derived genera, *Websteria* and *Egleria*. In these three genera, when the associated scale is separated from the spikelet by a developed shoot in its axil, the ultimate inflorescence unit is defined as the spikelet only.

In Group I, the definition of the ultimate inflorescence unit in each case makes for a visibly distinct body. (In those species where spikelets are clustered into a head, dissection is necessary to disclose the body but there is no question what parts should or should not be included in each case.) Note that in the two cases where the subtending bract is included in the unit, this necessarily includes the small portion of the rachis axis to which the bract and the rachilla are attached.

In Group I, the spikelet has a monopodial rachilla (Fig. 11a). I cannot agree with those authors from Pax (1886, 1887), Schulz (1887) and Celakovsky (1887) to Mora (1960) and Schultze-Motel (1964) who consider the spikeletlike structure of the Rhynchosporeae to be cymose and its rachilla to be sympodial, that is, that each flower terminates the rachilla internode below it and the next internode is a new branch which also terminates in a flower (Figs. 11b–11c). In this case, the glume which apparently subtends a flower would really subtend the new branch forming the next rachilla internode. These authors therefore call the spikeletlike structure a “partial inflorescence,” or “Scheinährchen” (pseudospikelet), not a spikelet. Also, I cannot see any evidence that the Cypereae and Scirpeae are any different from the Rhynchosporeae in this respect, yet Pax and Mora consider the units in these tribes to be true racemose spikelets with monopodial rachillas. (Schultze-Motel considers the spikeletlike units of these tribes

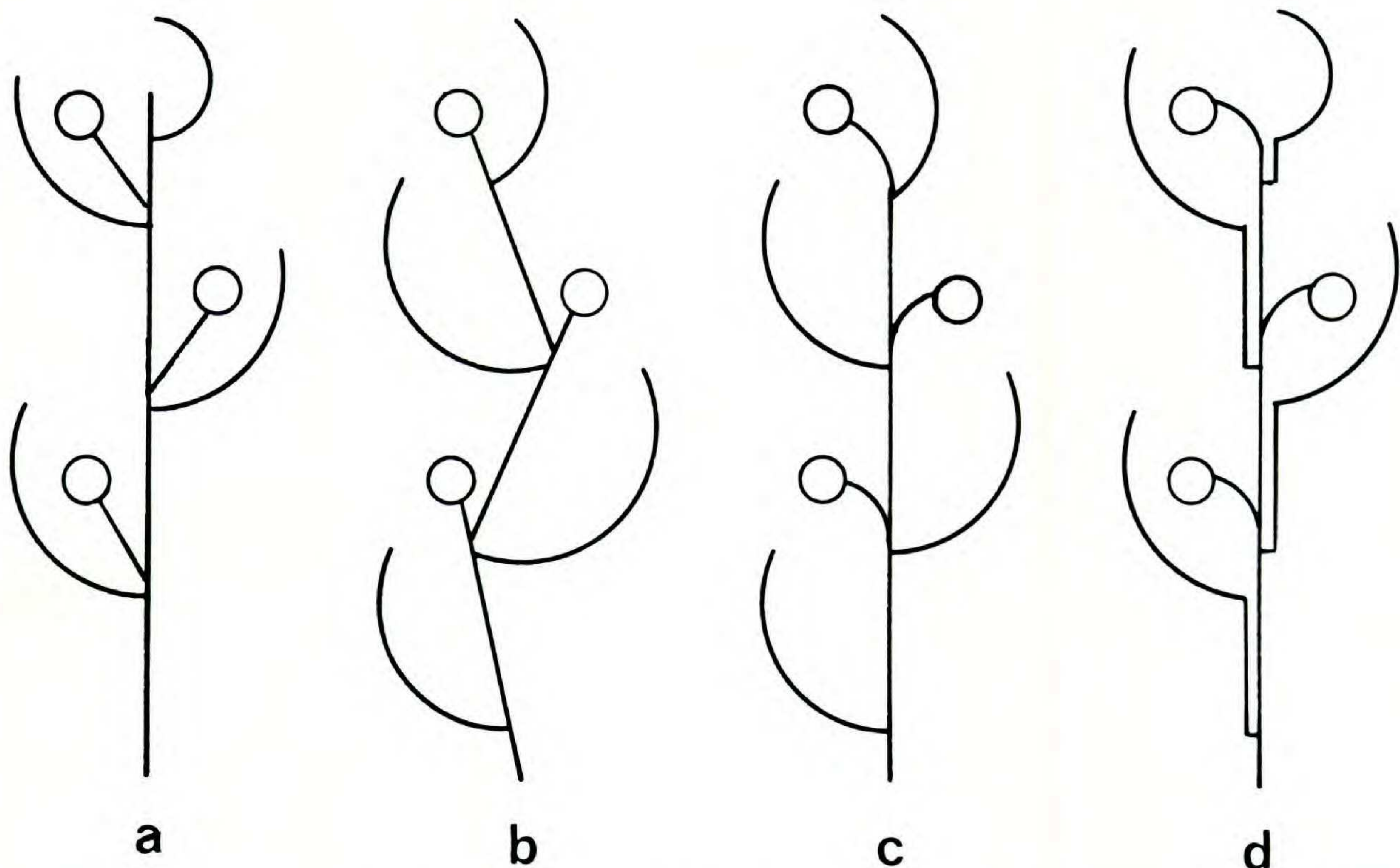


FIGURE 11. Branching patterns of spikelets of Group I under hypotheses of monopodality and sympodality.—a. Monopodial rachilla, true spikelet.—b. Sympodial pseudorachilla, scorpioid cyme.—c. Sympodial pseudorachilla with the pseudorachilla straight.—d. Sympodial pseudorachilla with recaulescence (adnation) of basal part of each glume to the axis which it subtends.

also to be cymose.) Mora says the decisive indication is whether the rachilla has a terminal flower at its tip or not; if it does, the structure is cymose (i.e., the rachilla is sympodial). As will be seen in various parts of this and the following paper (Eiten, 1976), an apparent terminal position of a flower in the Cyperaceae is no indication that it really is so; rather, it may well be pseudoterminal, that is, lateral.

In an inflorescence of the type supposed by Pax, Schulz, Celakovsky, Mora, and Schultze-Motel to be a scorpioid cyme,³ each glume would be on the opposite side of the stem from the flower (Figs. 11b–11c). (The same would be true for the helicoid cyme in Schultze-Motel's conception of the inflorescence unit of the Scirpeae.) Since the glumes are really on the same side of the rachilla as their flowers, appearing to subtend them, this is explained by assuming recaulescence

³ These authors invariably call this cyme a "Fächer" (rhipidium), which is a scorpioid cyme with all its branches lying in one plane. The branches, each terminating in a flower, in the distichous spikelets of the Cypereae do lie in one plane, but those of the Scirpeae and Rhynchosporeae do not since the flowers in these tribes are spirally arranged. To be consistent with their concept of a cymose structure, these authors should call the units in these two tribes a "Wickel" (cincinnus). Schultze-Motel (1964) considers the spikeletlike structure of the Rhynchosporeae and Cypereae to be a rhipidium also, but that of the Scirpeae he calls a "Schraubel" (bostryx), which is a helicoid cyme with the consecutive branches all arising on the same side and each lying at a transverse or oblique angle to its predecessor, not in the same plane. (Its diagram would be like Figs. 11b–11c, but with all the flowers on the same side of the rachilla.)

(Troll, 1964: 127), that is, adnation or concrescence of the basal part of the glume to the next internode, in this case to the supposed new branch that arises in the axil of the glume (see figure in Celakovsky, 1887). The adnate part of the glume is assumed to be narrow so that with the rachilla segment it would look like a single stem. The free part of the glume would then be on the same side of the axis as the *following* flower, appearing to subtend it (Fig. 11d).

I examined cross and longitudinal sections of the spikelets of three species of *Rhynchospora* and a species of *Cyperus*. (*Rhynchospora* sp.: Hatschbach 14942, Brazil, Paraná, Mun. Bituruna, 17 Oct. 1966. *Rhynchospora* sp.: Hatschbach 14824, Brazil, Paraná, Mun. Piraquara, 10 Oct. 1966. *Rhynchospora corniculata* (Lam.) A. Gray: Swayne & Bailey 1112, U.S.A., Illinois, Gallatin Co., 3 Aug. 1950. *Cyperus* sp.: Robinson 6192, Zambia, Chakwenga Headwaters, 100–129 km E of Lusaka, 10 Jan. 1964.) The many essentially parallel “scattered” vascular bundles in a culm are reduced in a rachilla to a few bundles crowded together in the central part of the axis, forming a strand that often appears topographically (but not histologically) like a stele. Branches from this central strand go to the flowers while other branches go to the glumes. The number of branches (traces) going to a single glume depends on how many vasculated veins the glume possesses; often there is only a single trace going to the midvein. In a monopodial rachilla axis, the glume trace(s) leave the central strand at a wide angle below the point where the flower trace(s) leave it that go to the subtended flower. The region along the stem where all these traces leave the central strand and go to one flower and its subtending glume would then be defined as a single node. In a recalcrescent sympodial rachilla axis, the glume trace(s) would leave the central strand and would then lie parallel to it in the ground tissue through the next internode before leaving the rachilla to enter the free part of the glume. A cross section of an internode in this case would show the central strand *plus* the one or more glume traces lying around it or on one side of it (Fig. 11d). However, all the sections examined showed only the central strand; at no level were there any other bundles in the ground parenchyma except where, as explained, traces left at a wide angle to go directly to a glume or flower at a node. I must conclude from these preliminary observations that there is no anatomical evidence for recalcrescence and therefore sympodality.

It is true that Arber (1925: 137–148) has shown that in cases of adnation between a stem and a leaf, where the leaf remains a flat lamina and leaflike in its lower part where the stem is adnate, as well as above, the vascular anatomy in the lower part is wholly foliar, there being no trace of a separate stem stele. She gives drawings of *Tilia* (peduncle and bract) and of *Ruscus* and related genera (peduncle and “phyllode,” which she interprets as a prophyll bract). One can suppose that the stem bundles in these genera either disappeared in evolution or fused with the midvein of the bract. In our sedge spikelet examples the supposed recalcrescent part is stemlike, not foliar, but it is possible of course that recalcrescence has really occurred but its anatomical evidence has disappeared because, in this case, the leaf bundles became lost or fused with the stem bundles. But if so, the anatomy would be exactly like that of a monopodial stem so that it cannot be used to distinguish between the two possibilities. When there

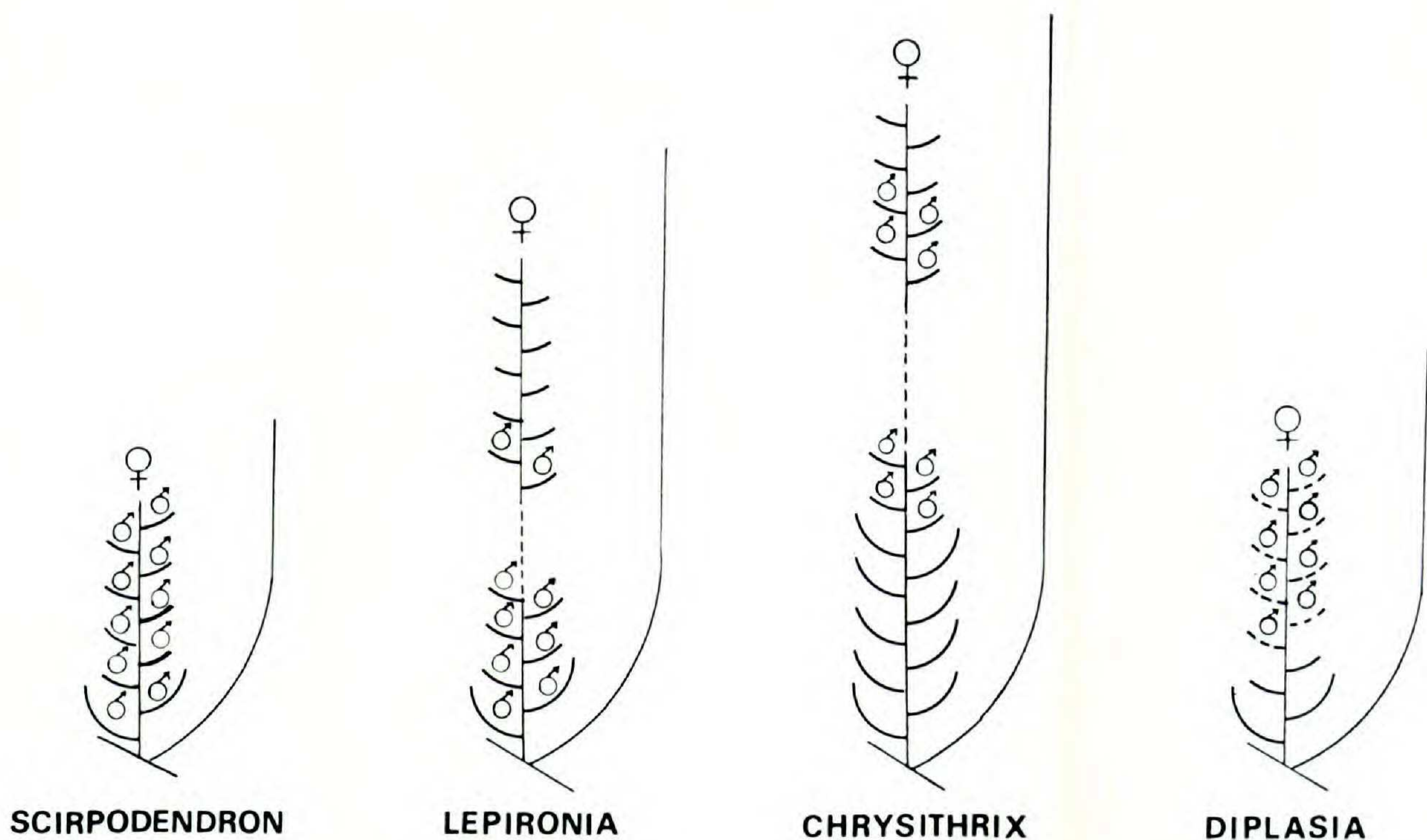


FIGURE 12. Branching patterns of inflorescence units of genera of Group II. The female symbol at the apex of the rachilla represents an apparently terminal female flower of one pistil. The broken-line curves represent glumellas which are supposed to have disappeared in evolution. The broken-line portion of the rachilla represents a continuation of the same arrangement of glumes and flowers. In *Chrysithrix* the basal part of the axis whose tip is the rachilla is the culm (although this is not shown) and is thus similar to *Eleocharis* in this respect.

is no definite evidence that an axis is sympodial, it is morphologically simpler and more logically correct by Occam's Razor to consider it monopodial. (See footnote 5.)

GROUP II

The inflorescence is formed of one or more pseudospikelets. The axis of the pseudospikelet is a continuation of the axis of the culm or of one of its branches of first or higher order. Each pseudospikelet possesses many pseudanthia (a reduced axis with flowers, each looking like a single bisexual flower). Each pseudanthium is hidden by a subtending glumelike covering bract and consists of a very short axis bearing an apparently terminal pistil; beneath this perianthless female flower the axis bears several to many glumellas. A glumella is either empty or bears in its axil a male flower consisting of a single stamen (Figs. 12-13). The two basal glumellas (the most external ones) are always lateral, folded, and have pilose keels. The other glumellas are thinner and glabrous, and are not keeled but flat or slightly curved. In some species of *Hypolytrum*, the two keeled lateral glumellas are the only glumellas present. They may be partially or wholly fused by their margins.

Examples of this group are the following genera, all of the tribe Mapanieae (= Hypolytreae): **Scirpodendron*, **Lepironia* (including *Chorizandra*), *Diplasia*, *Exocarya*, *Mapania*, **Thoracostachyum*, *Mapaniopsis*, and *Hypolytrum*.

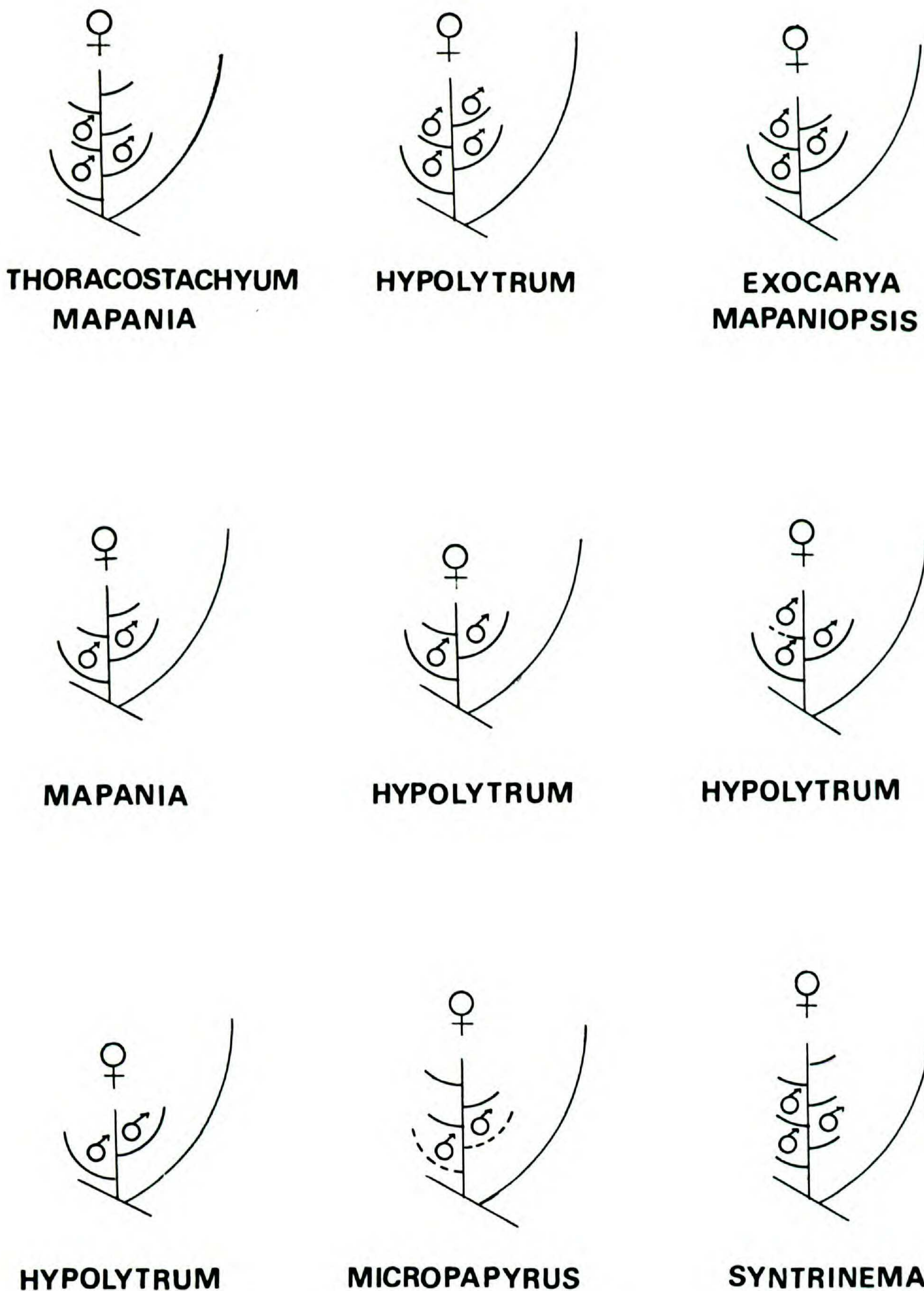


FIGURE 13. Branching patterns of inflorescence units of genera of Group II, showing types of reduction in number of glumellas and flowers. Note that different species of the same genus may be slightly different and that more than one genus may have the same pattern.

Besides these genera which are typical of the Mapanieae, there are three peculiar ones which are also considered to belong to Group II.

The inflorescence of **Chrysithrix* is not made up of pseudospikelets but rather of a single terminal pseudanthium whose axis is the continuation of the axis of the culm; therefore this pseudanthium does not arise in the axil of a subtending covering bract. The glumellas are larger, thicker, glabrous, and not keeled; they could more properly be called glumes. The outer glume extends beyond the pseudanthium and does possess a thick keel at its base. (This outer glume is considered an extension of the culm by some authors, which would then make the axis of the pseudanthium a lateral branch.)

The genus *Micropapyrus*, described in detail in the following article (Eiten, 1976), also forms pseudospikelets but they contain only 1–2 pseudanthia and the glumellas are in the form of bristles. The inflorescence is made up of sympodial branches with wide-spaced pseudospikelets.

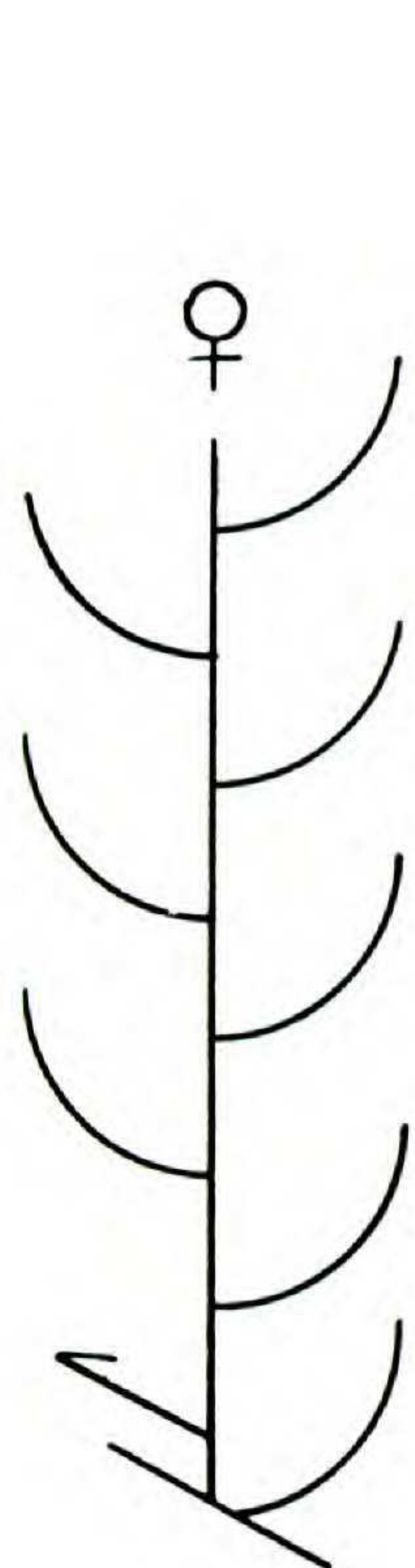
The genus *Syntrinema*, also described in detail in the next article (Eiten, 1976), presents an inflorescence of pseudospikelets united in headlike spikes. The glumellas are free in the lower pseudanthia and are in the form of bristles. The distal pseudanthia in a pseudospikelet are male and do not possess a female flower. The glumella bristles here are lacking or are possibly fused with the filaments which form a column to which are attached the free anthers.

The ultimate inflorescence unit in Group II, then, is of two types: (1) Pseudanthium plus its covering bract. (2) Pseudanthium alone. This is found in only *Chrysithrix*, which has no covering bract.

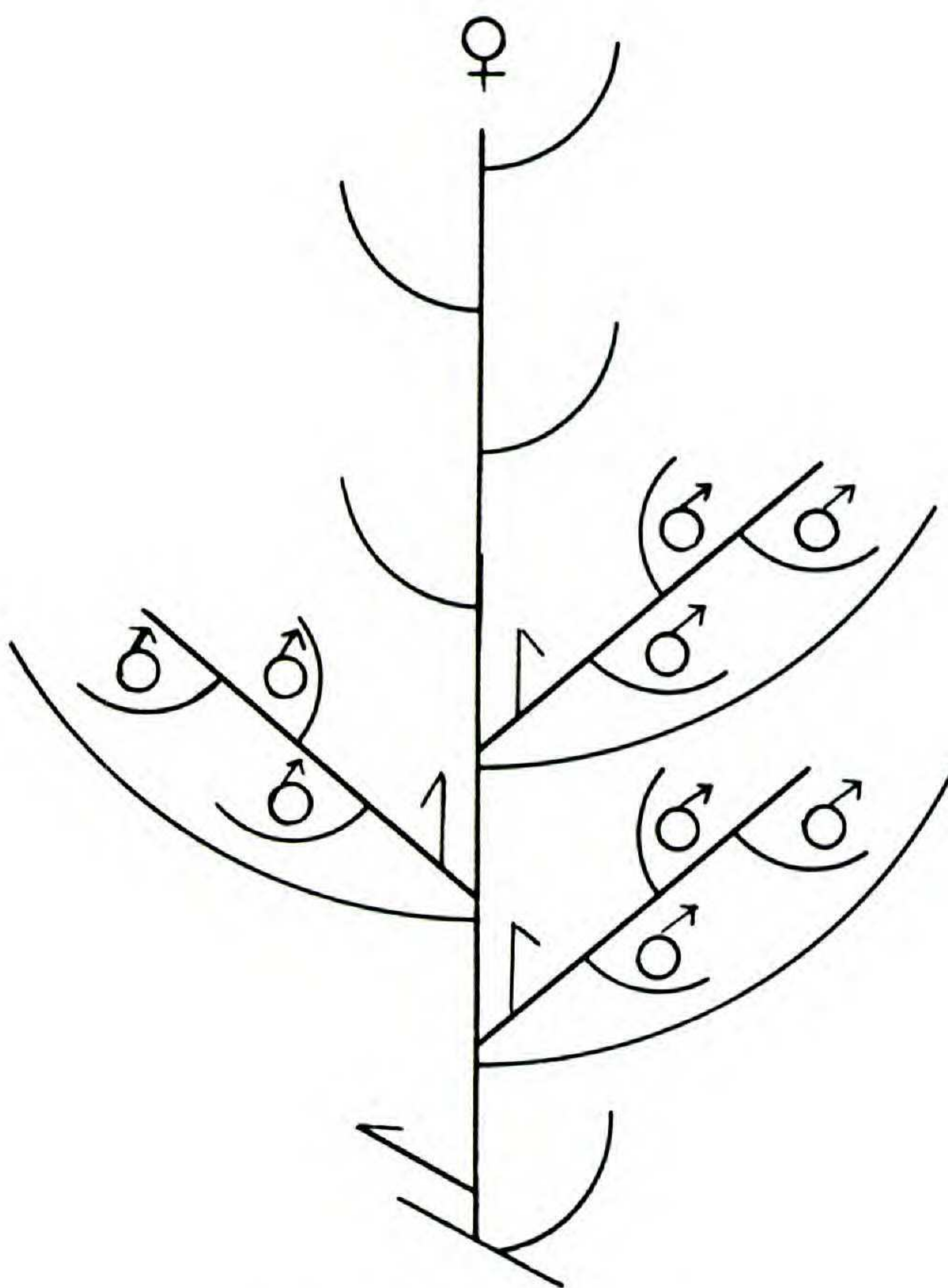
Before taking up Group III, it is necessary to discuss the inflorescence units of the genus *Scirpus*. The interpretation of the bristles of this genus by certain cyperologists, such as Schultze-Motel (1964), has led to the hypothesis that *Scirpus* is derived from the Mapanieae.

In the classical theory, the bristles of *Scirpus* are considered to be a perianth. Since 1888, when Goebel introduced the idea that the "flower" of *Scirpodendron* is an inflorescence, that is, a pseudanthium, this idea was extended to the whole tribe Mapanieae, to which *Scirpodendron* belongs, and afterwards to the tribes Scirpeae, Cypereae, and Rhynchosporae. According to this theory, what appears to be a simple flower in the genera of Group I is really a reduced inflorescence simulating a true flower. The pistil and each stamen are unisexual flowers. There appears to be a reduction series starting with *Scirpodendron*, *Lepironia* and *Chrysithrix*, passing through *Mapania* and *Hypolytrum* with fewer parts, and arriving at *Scirpus* by way of species such as *S. membranaceus* Thunb. and *S. isolepis* Boeck. In these species, two hypogynous, wide, glabrous scales (supposedly homologous with the bristles in other species of *Scirpus*) that are lateral in position, folded along the middle but not keeled, are in the same position as the two lateral, keeled glumellas of *Hypolytrum* (see Clarke, 1909: tab. XLVII, 12; tab. XLVIII, 4; tab. LII, 14, 15, 17). Therefore, the floral diagram of these species of *Scirpus* is equal to that of some species of *Hypolytrum* (see Clarke, 1909: tab. CIV, 5, 10; tab. CV, 5, 10, 18; tab. CVI, 7, 12).

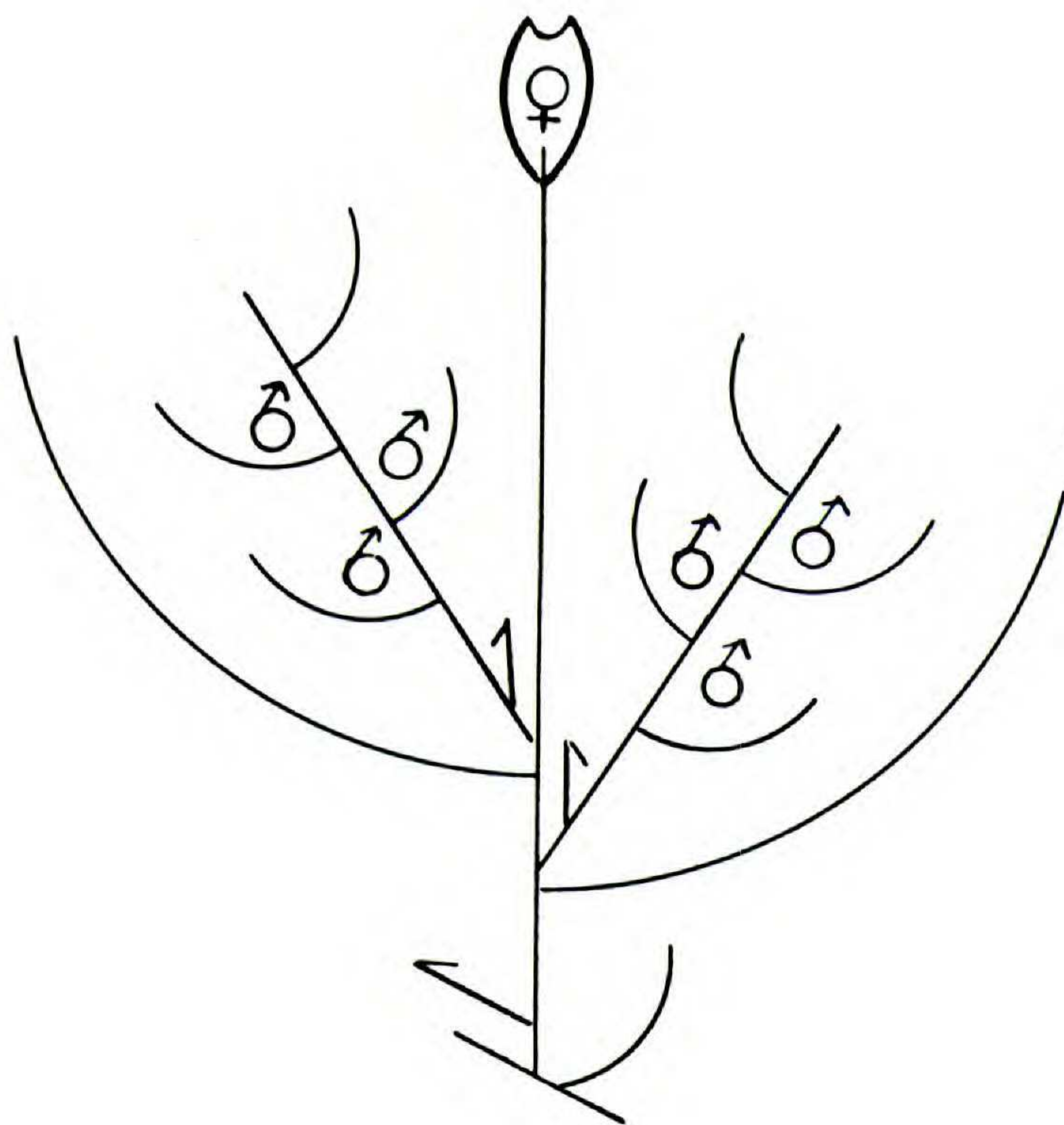
But only this similarity is not sufficient to conclude that *Scirpus* evolved from *Hypolytrum* or from the Mapanieae in general. These two genera are not



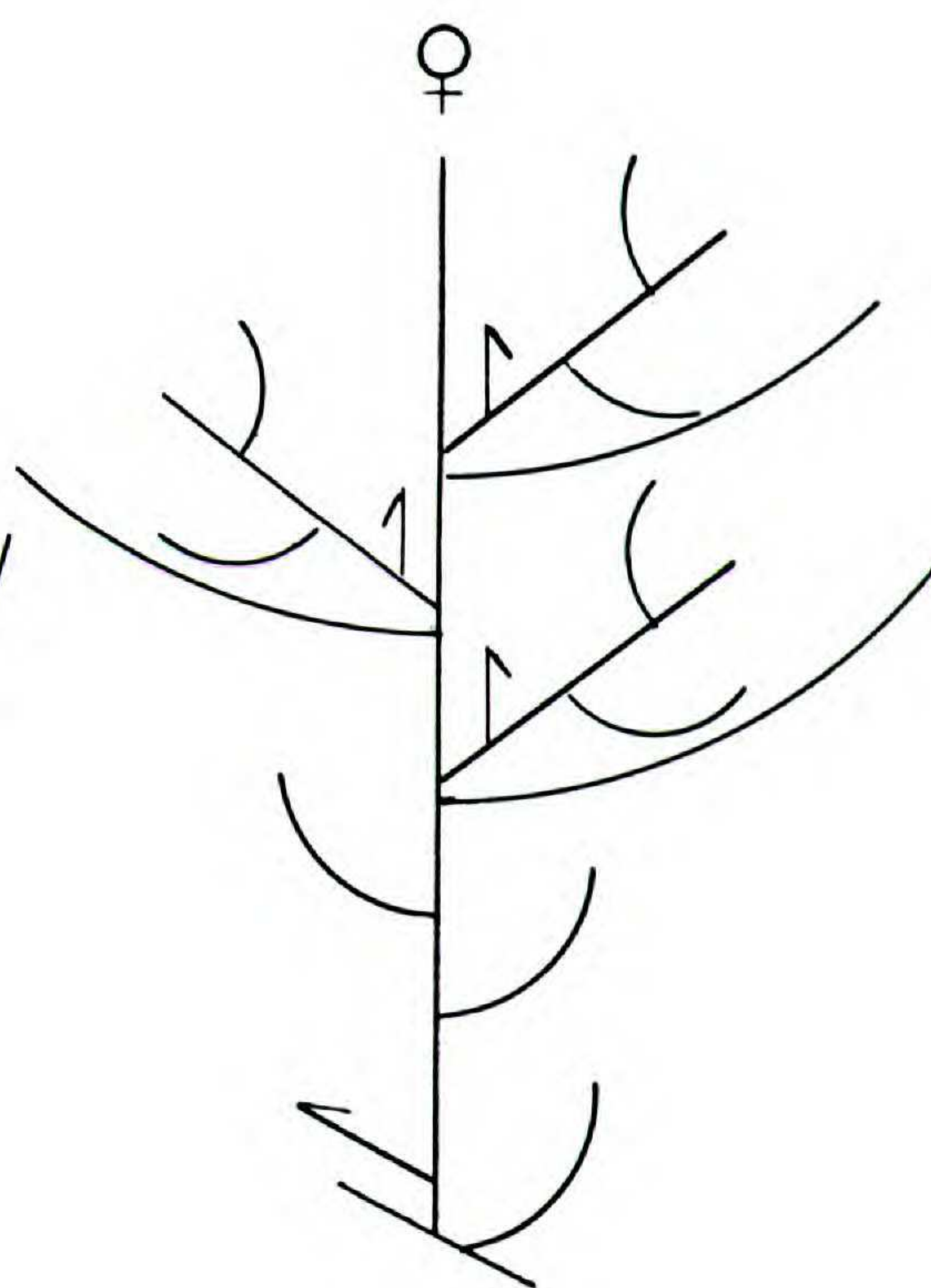
DIPLACRUM



DIPLACRUM



BISBOECKELERA



CALYPTROCARYA

sufficiently similar in other characters to be considered related. The lateral scales of *S. membranaceus* and of *S. isolepis* appear to be a derived form within *Scirpus* and not a primitive form of this organ. (In *Fuirena* and in certain lines in the Compositae, the same thing seems to have occurred: bristles have evolved to laminar structures.) The similarity in the placement of the laminas in these two species of *Scirpus* and in *Hypolytrum* does not indicate a phylogenetic connection but is due to spatial considerations of growth, if it is not merely a coincidence.

It is also necessary to consider *Dulichium* here since Schultze-Motel (1959, 1964) claims that its inflorescence unit is a pseudanthium and its bristles are bracts. He calls attention to the fact that the vascular traces to the bristles on the adaxial side of the pistil separate at a higher level than the traces going to the abaxial bristles which are next to the stamens. The two groups of bristles, as visibly separate organs, also separate from the subpistilar axis at different levels. Therefore he claims that the two groups of bristles cannot belong to the same ring and so cannot be calyx parts, and therefore the pistil and stamens cannot be a flower and must be a pseudanthium (synanthium). In the first place, even if the bristles really were bracts, this does not prevent the pistil and stamens from being parts of a single flower because, as is evident from Schultze-Motel's anatomical drawings, the traces of the adaxial bristles arise from different and independent bundles than those from which the stamen traces arise. They do not arise above and from the same bundles as the stamen traces. If they did, this would be an indication that the structure is not a single flower. In the second place, the bristles could well be part of a single ring as is here considered to be the case in *Scirpus*. It is certainly possible that the pressure on the adaxial side of the subpistilar (i.e., floral) axis against the axis (rachilla) from which it sprang caused the base of the adaxial bristles to fuse to the floral axis. If this happened, then, as frequently occurs in flowers, the bundles in the fused parts also fused basally. Schultze-Motel denies this possibility but without any good evidence as far as I can see. When the evidence is not conclusive one way or the other, the most logical thing is to support the simplest hypothesis that the bristles are a perianth ring and the flowerlike structure in *Dulichium* is a true flower. Therefore, the genus belongs in Group I. Since *Dulichium* has characteristics of Cyperaceae, Scirpeae, and Rhynchosporae without fitting comfortably in any one, the question is still open as to its tribal position or as to whether it should constitute a separate tribe as Schultze-Motel believes.

GROUP III

The inflorescence is capituliform but without a central axis or a flat, compound receptacle. The head is composed of branchings of several orders, the whole ex-

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FIGURE 14. Branching patterns of inflorescence units of genera of Group III. In *Diplacrum*, the inflorescence unit which bears a pistil usually has male-flowered spikelets as lateral branches (right) but sometimes these are absent (left). In *Bisboeckelera* the pistil is contained in an utricle. The branching pattern shown for *Calyptracarya* represents a specimen seen in which there were no flowers developed in the lateral spikelets. Usually, male flowers of one stamen are borne in the axils of the glumes.

tremely condensed. At the tip of each branch there is an apparently terminal pistil, and below the pistil, there usually occur one or more spikelets of male flowers, the spikelets arising from the same axis that terminates in the pistil. Each male spikelet is subtended by a glumiform covering bract and the rachilla axis just below the spikelet bears a prophyll (Fig. 14).

This group is exemplified by the following genera: *Becquerelia*, *Diplacrum*, *Bisboeckelera*, and *Calyptracarya*.

In *Becquerelia*, there are usually three male spikelets on an axis (Nees, 1842: tab. 27), but I have seen from 0–7.

In *Calyptracarya*, I have always seen only three male spikelets (Nees, 1842: tab. 28). In some cases, all three lack stamens (Fig. 14). The empty scales on the axis that ends in a pistil are below the male spikelets.

Diplacrum, as is demonstrated in the following article (Eiten, 1976), possesses a great variability in the pattern of its ultimate branch orders. But the basic pattern is that of Group III. On the axis that apparently terminates in a pistil there are 0–3 male spikelets.

In *Bisboeckelera* (= *Hoppia*) two male spikelets occur below the apparently terminal pistil. The distal empty glumes are fused forming a utricle that encloses the pistil.

The pistil in these genera is *apparently* terminal but may really be only pseudoterminal as Celakovsky (1887) observed.

The ultimate inflorescence unit in this group consists of an axis (rachis) apparently terminating in a pistil, the 0–3 male spikelets (with their adjacent prophylls and subtending bracts) immediately below the pistil, the empty scales (which enclose the pistil) on the rachis just above the male spikelets or in the case of *Calyptracarya*, just below the spikelets. When the prophyll of the rachis and its subtending bract are next to the parts already described (not separated by further branches on the rachis), they too are included in the unit. In complicated cases such as some of the branching patterns shown for *Diplacrum* in the following article (Eiten, 1976), where a rachis with pistil has not only branches which are male spikelets but also other lower branches immediately adjacent, of the same order, and bearing distal pistils, then these female branches (with their prophylls and subtending bracts) are considered to be *separate* ultimate inflorescence units. These lateral female branches may have no male spikelets below their pistil (see Eiten, 1976: figs. 127–128, 130–133, 135 upper branch) or they may have 1–2 male spikelets (see Eiten, 1976: figs. 134, 135 lower branch, 136). In these cases, the unit made up of the original main rachis and its pistil and immediately adjacent male spikelets does not include the prophyll and subtending bract of this main rachis since these are separated from the rest of the unit.

Thus there are two types of ultimate inflorescence units in Group III, those with and those without the immediately adjacent prophyll and subtending bract. In Group III the unit as just defined does not usually make up a visibly distinct unit in the inflorescence head before dissection, but it is unambiguously defined as to what parts it includes.

The genus *Scleria* in classifications of the family is usually placed in the same tribe as *Becquerelia* and *Diplacrum*. In fact, some authors include *Diplacrum* in

Scleria (Koyama, 1961; Kern, 1961; Raymond, 1966). This relationship between *Scleria* and the other two genera has not yet been proved but is only suggested by the similar habit. In the inflorescence of *Scleria* species there are multiflowered spikelets of only male flowers and also spikelets with pistils. The latter have several empty glumes below the pistil and are of three types:

1. Bisexual spikelet (also called androgynous spikelet). At the side of the pistil, there is an apparently terminal axis with glumes subtending developed male flowers (Figs. 15–16, *Scleria virgata* (Nees) Steud., Schwacke 41830, Brazil, [RB]). This type of spikelet is also illustrated by Clarke (1909: tab. CXXIV, 3; tab. CXXV, 4) and Robinson (1966) figs. 1–8).

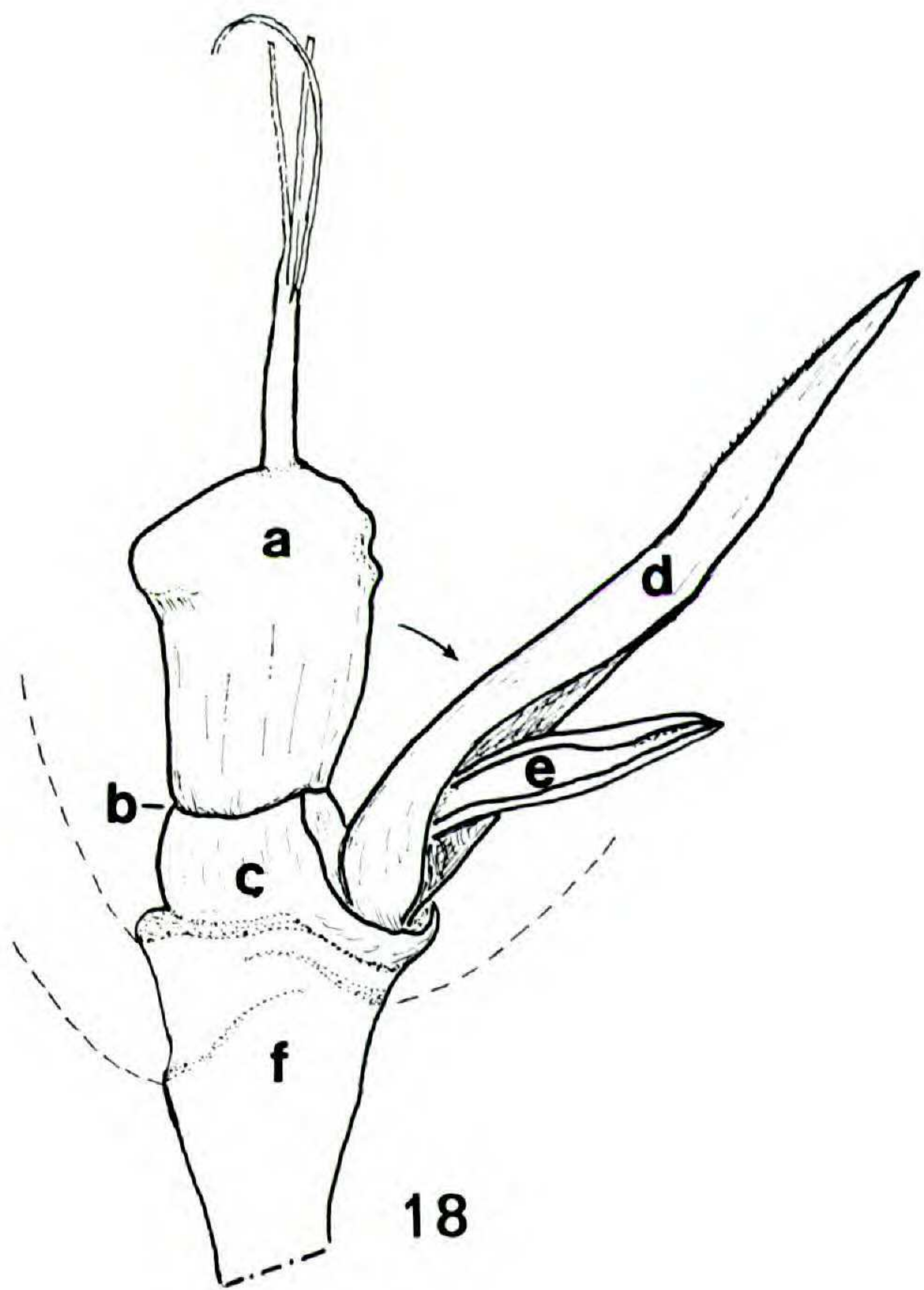
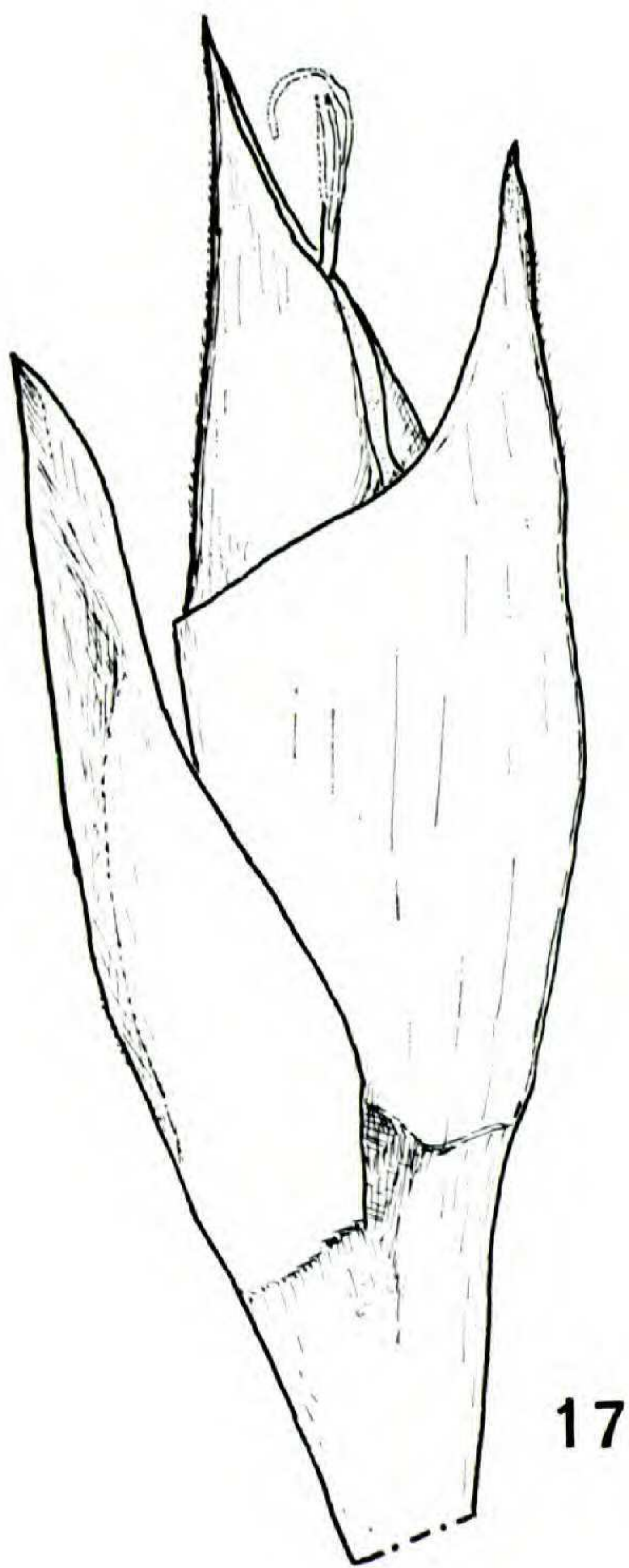
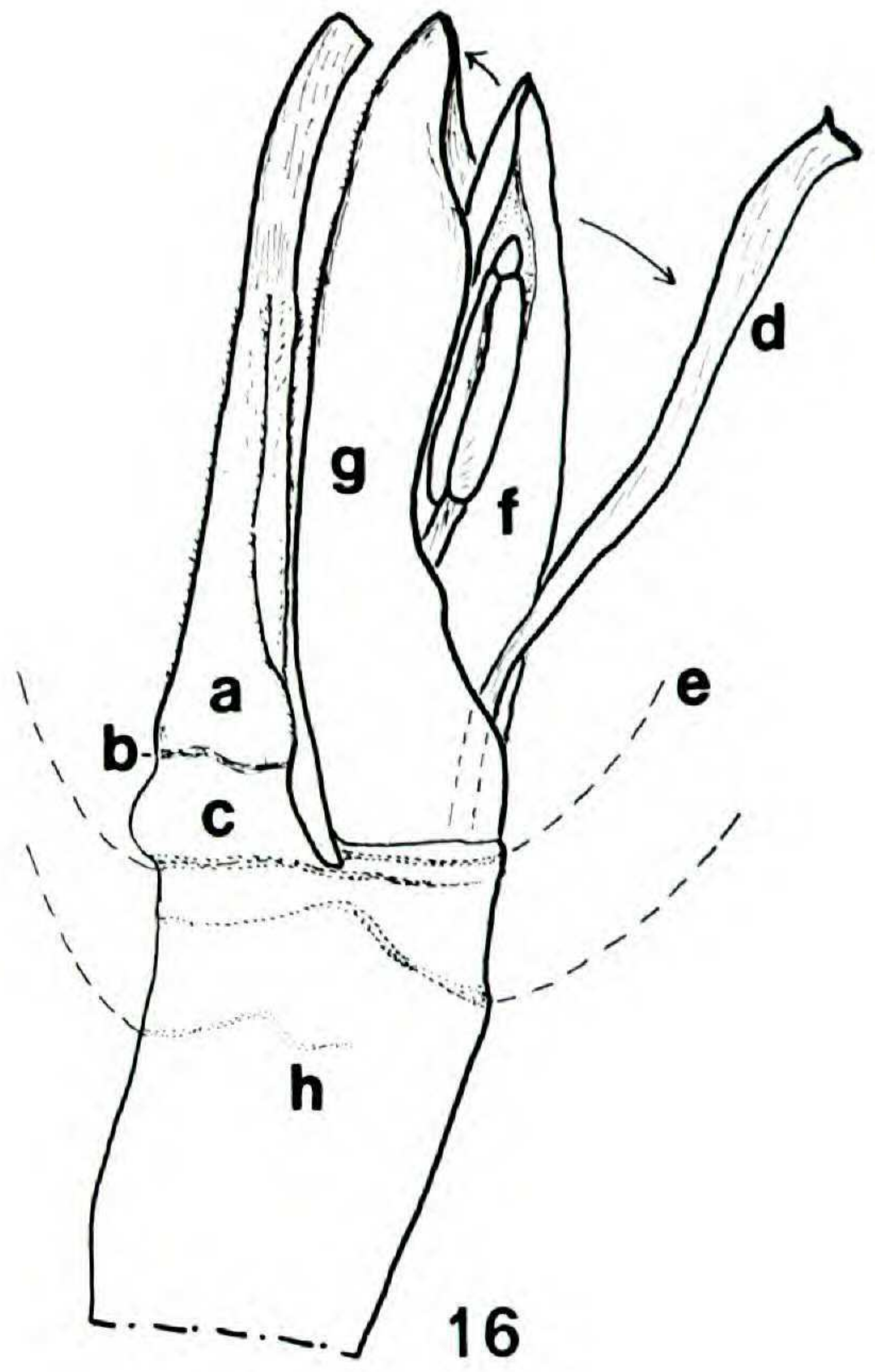
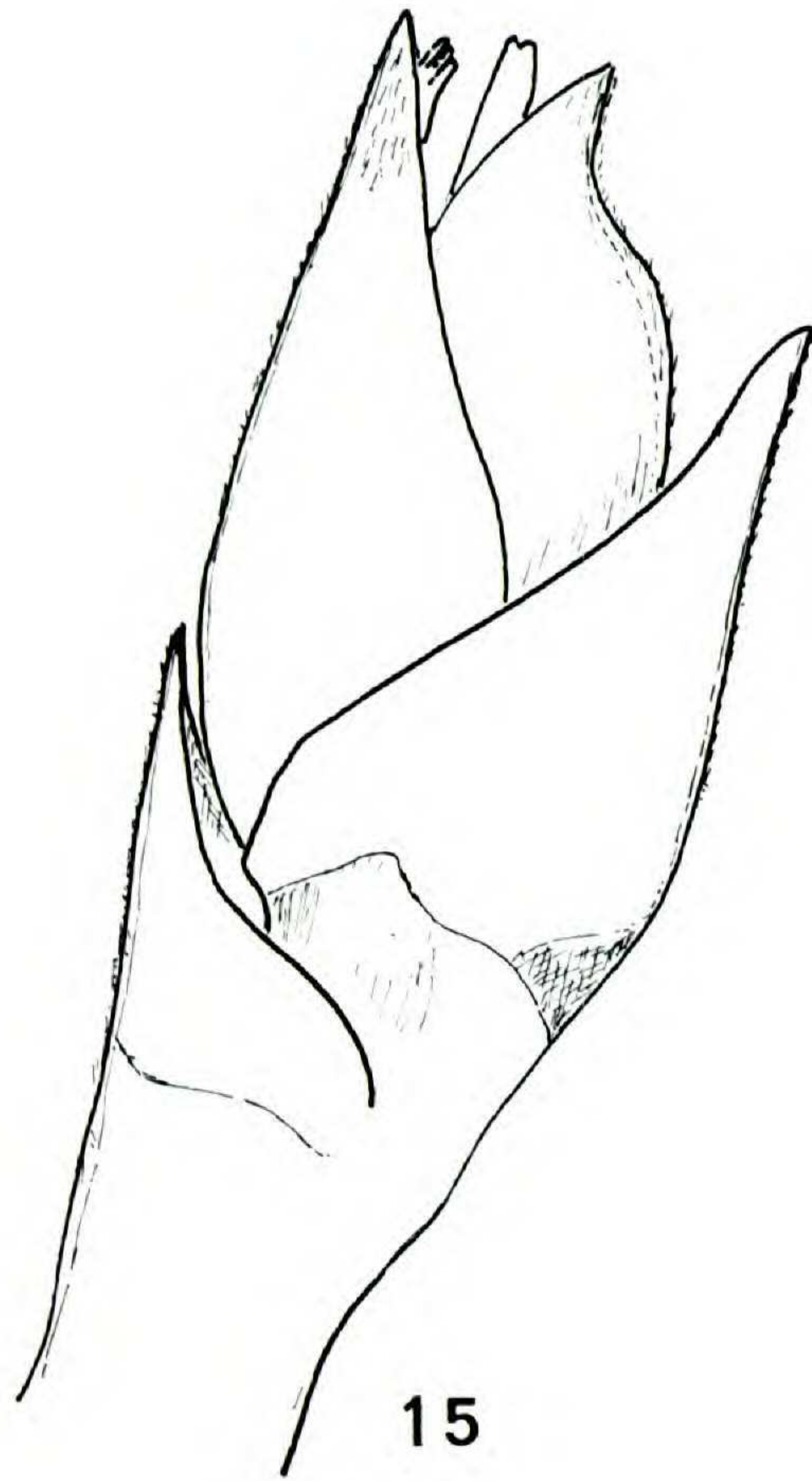
2. Female spikelet with male vestige (also called “subandrogynous”). This structure is similar to the first but the male part is reduced to a few enrolled empty glumellas (Figs. 17–18, *Scleria lacustris* Wright, Rodrigues & Coelho 1932, Brazil, Amazonas [INPA]). The same structure, with the vestigial male part even smaller than that shown in Fig. 18, is illustrated by Clarke (1909: tab. CXXVII, 5), by Nees (1842: tab. 26, nos. 19 & 22), and by Robinson (1966: fig. 9, no. 7).

3. Female spikelet. There is no male vestige at the side of the pistil. Illustrations of this type are found in Nees (1842: tab. 22), Clarke (1909: tab. CXXXI, 5), and in Robinson (1966: figs. 11–16).

There are two interpretations of the structure of *Scleria* spikelets which contain pistils. One, held by Nees (1842), Bentham (1883), Holttum (1948), and Koyama (1961), states that the spikelet has only one axis from which arise laterally all the flowers, including the pistillate flower. The male part then corresponds to the distal portion of this axis. The other interpretation, held by Pax (1886), Schultze-Motel (1964), and Koyama (1967, 1969), states that there are two axes in the bisexual spikeletlike structure, one terminating in the pistil and the other, of immediately higher order, arising laterally from the first axis near the base of the pistil and bearing the male flowers.

There is no evidence in the genus Scleria itself which supports the second interpretation. At the base of the male part there is no lamina with the form or position of a prophyll which would indicate a new branch. I could find none examining many species of *Scleria*, and Nees (1842), Clarke (1909), and Robinson (1966) do not indicate any in their descriptions and drawings of *Scleria* species. Koyama (1969) illustrated a prophyll at the base of the male part in his branching schemes of *Scleria* in his Figs. 6 and 27. These are based on his Fig. 4, a realistic explosion drawing of *Scleria verticillata*, where he shows a small unmarked scale just above the achene which would correspond to the necessary prophyll. This drawing is obviously redrawn from Fig. 3C of his 1961 paper where this scale does not appear, and where he upholds the lateral position of the female flower.

To justify the terminal position of the pistil, Koyama, in his present view, states that the vascular bundles in the rachilla go in a straight line to the pistil. But in the uniflorous spikelets of *Cyperus* sect. *Kyllinga*, where the flower is undoubtedly lateral, the vascular bundles in the rachilla also go in a straight line to the pistil which appears to be terminal (see Clarke, 1909: tab. I, 3; Kükenthal,



1935–1936: figs. 62C, 62J, 64H, 64K). Besides this, the distal part of the rachilla bends laterally to continue along the side of the apparently terminal pistil, appearing to be a lateral branch when it really is not. The same thing occurs in *Uncinia* and *Carex*, where the lateral female flower also appears to be terminal (see Kükenthal, 1909: fig. 7C; Mora, 1960: fig. 51; Kukkonen, 1967: fig. 1).

Those who support the interpretation that there are two axes in the bisexual spikelet of *Scleria*, such as Koyama (1969), appeal only to indirect evidence. They maintain, from the general aspect and some other characters, that *Scleria* is related to the four genera cited in Group III, especially to *Becquerelia* and *Diplacrum*. Therefore, by analogy, the continuation of the axis which bears the male flowers in the bisexual spikeletlike structure of *Scleria* would be a new branch as it is in the genera of Group III. In these genera there is usually more than one male spikelet below the pistil. *Scleria*, then, would be a reduction, having only one male spikelet, or none by abortion. But the question is exactly whether *Scleria* really is related to the genera of Group III.

I have examined hundreds of collections of *Scleria*, representing species of all the sections of the genus, dissecting the spikelets and making analytical drawings of the branching patterns. I cleared the tissue of spikelet axes (rachillas) to follow the vascular bundles, and also made longitudinal and cross sections. However, the anatomy of mature spikelets does not clarify the problem; it is not possible to know when a vascular bundle forks in the spikelet axis, which branch is the lateral branch, and which branch continues the main axis. (See footnote 5.) Since it was not possible to obtain direct evidence at the level of the "spikelets" (i.e., the ultimate inflorescence units, which contain the last branch orders of the inflorescence), where the internodes and laminar organs are highly reduced, I analyzed the lower branch orders of the inflorescence, recording the branching pattern in diagrams. I noted certain patterns: (1) An axis which bears a pistil may arise from an axis which terminates in a purely male spikelet. (2) An axis which bears a pistil may arise from an axis which also bears a pistil. (3) An axis which terminates in a purely male spikelet may arise from an axis which also terminates in a purely male spikelet. (4) An axis which terminates in a purely male spikelet may arise from an axis which terminates in a bisexual spikeletlike structure, including those with the male part vestigial. (5) An axis which terminates in a bisexual spikeletlike structure may arise from an axis which also

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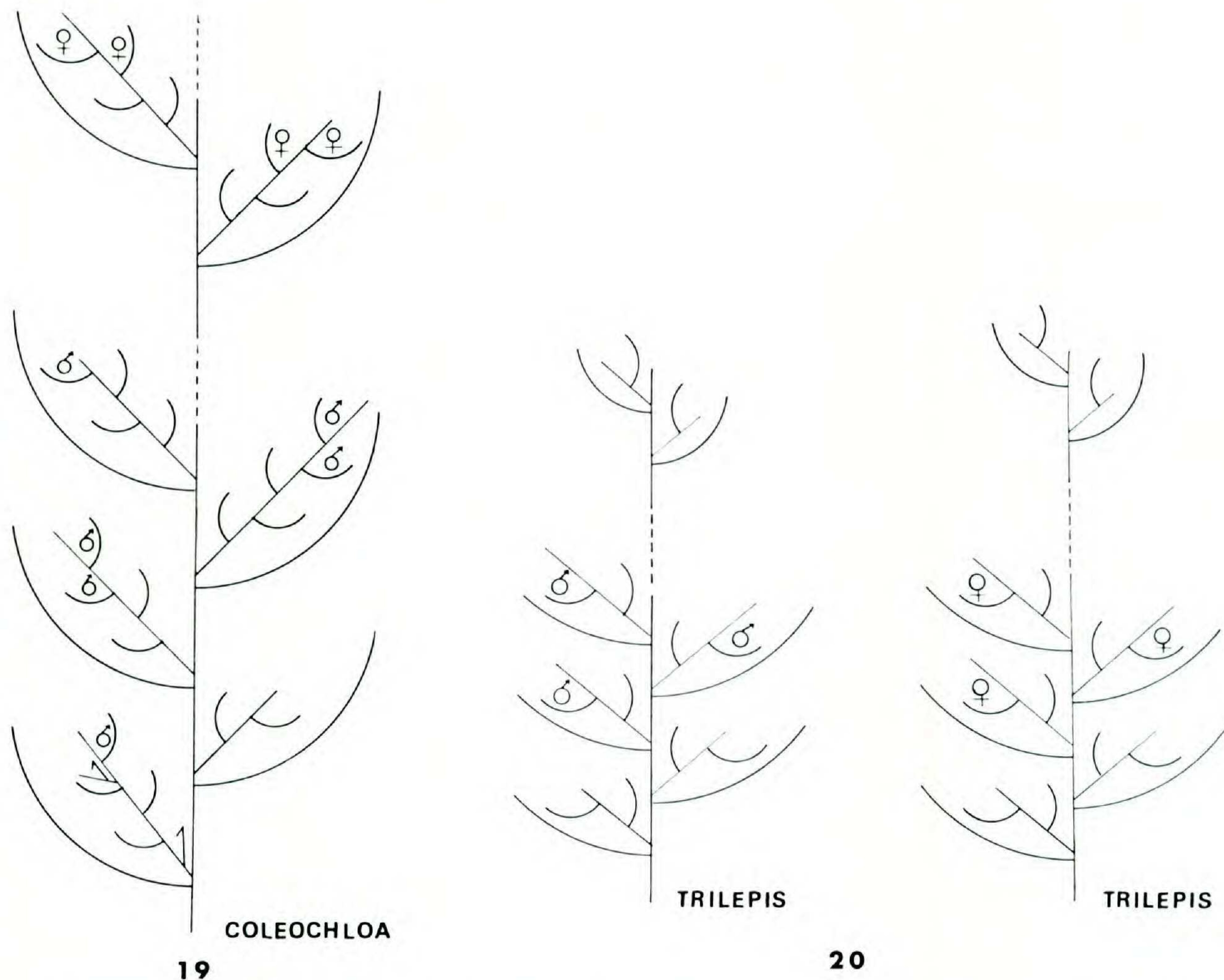
FIGURES 15–18. Aspects of pistil-containing spikelets of *Scleria*; $\times 8.9$ —15–16. *Scleria virgata* (Nees) Steud.; Schwacke 41830. In this species the male part is well developed and functional. Figure 16 shows the same spikelet as Fig. 15 but with the lower glumes removed (represented by broken lines); a = female flower of one pistil; b = abscission layer of flower; c = axis lateral to the rachilla and which terminally bears the pistil (floral axis); d = filament of lower male flower from which anther has fallen; e = position of glume which subtends lowest male flower; f–g = glumes subtending and enclosing upper male flowers; h = rachilla of spikelet.—17–18. *Scleria lacustris* Wright; Rodrigues & Coelho 1932. In this species the male part is vestigial, reduced to two small empty glumes. Figure 18 shows the same spikelet as in Fig. 17 but with the lower glumes removed (represented by broken lines); a = young fruit; b = abscission layer of fruit; c = axis lateral to the rachilla and which terminally bears the pistil (floral axis); d–e = empty glumes of the vestigial male part; f = rachilla of spikelet.

terminates in a bisexual spikeletlike structure. In all five patterns the presence of an evident prophyll indicates an undoubtedly new branch. The only pattern *not* found was an axis terminating in a purely male spikelet arising from an axis which bears a pure female spikelet, that is, one without an associated male vestige. Since this pattern was verified up to the penultimate branch order, it would be strange if it were inverted in the ultimate branch order. Therefore, in the bisexual spikeletlike structure, the male part would not seem to be a new branch which arises from an axis which terminally bears a pistil. These observations furnish direct evidence from the genus *Scleria* itself that the pistil in a bisexual spikeletlike structure is lateral, that is, that there is only one axis and so the structure is a true spikelet. This conclusion is strengthened by observations on *Scleria bracteata* Cav. and *S. cyperina* Kunth. In both, the pistillate spikelets are always on the basal branches of the inflorescence (Nees, 1842: tab. 24), that is, there is a tendency in the genus for the female part to be basal in relation to the male part. Mora (1960) also noticed this tendency in *Scleria*. There is another tendency within the family which supports the lateral interpretation of the female flower in *Scleria*. In genera in which there are true spikelets with all the flowers lateral and almost always bisexual, such as *Cyperus* and *Eleocharis*, when there is a reduction in the sexual parts, it is almost always the pistil which aborts, producing a male flower. When this happens, it always occurs in flowers in the upper part of the spikelet, the basal flowers remaining bisexual.

As to the supposed relation between *Scleria* on the one hand and *Bequerelia* and *Diplacrum* on the other, it is interesting to note that the typical branching pattern of the inflorescence of the two latter genera is one in which axes which terminate in male spikelets arise from axes which apparently terminate in pistils, exactly the only pattern which does not occur in *Scleria*.

The bisexual spikelet in *Scleria* is similar in its branching pattern to that of *Rhynchospora* (Fig. 1). However, I do not include *Scleria*, which always has unisexual flowers, in Group I because, characteristically, the flowers in the genera of this group are bisexual. (In the Rhynchosporae some but not all the flowers in a spikelet are male.) Although *Scleria* is similar to *Schoenoxiphium* and *Kobresia* in branching pattern and sex of flowers, I do not include it in Group VI because the female flower is not inside a utricular or semiutricular prophyll. Not being able to place *Scleria* in any of the six groups presented and not having irrefutable evidence as to what the structure of its ultimate inflorescence unit really is, I prefer to leave the position of the genus to be decided on the basis of future studies.

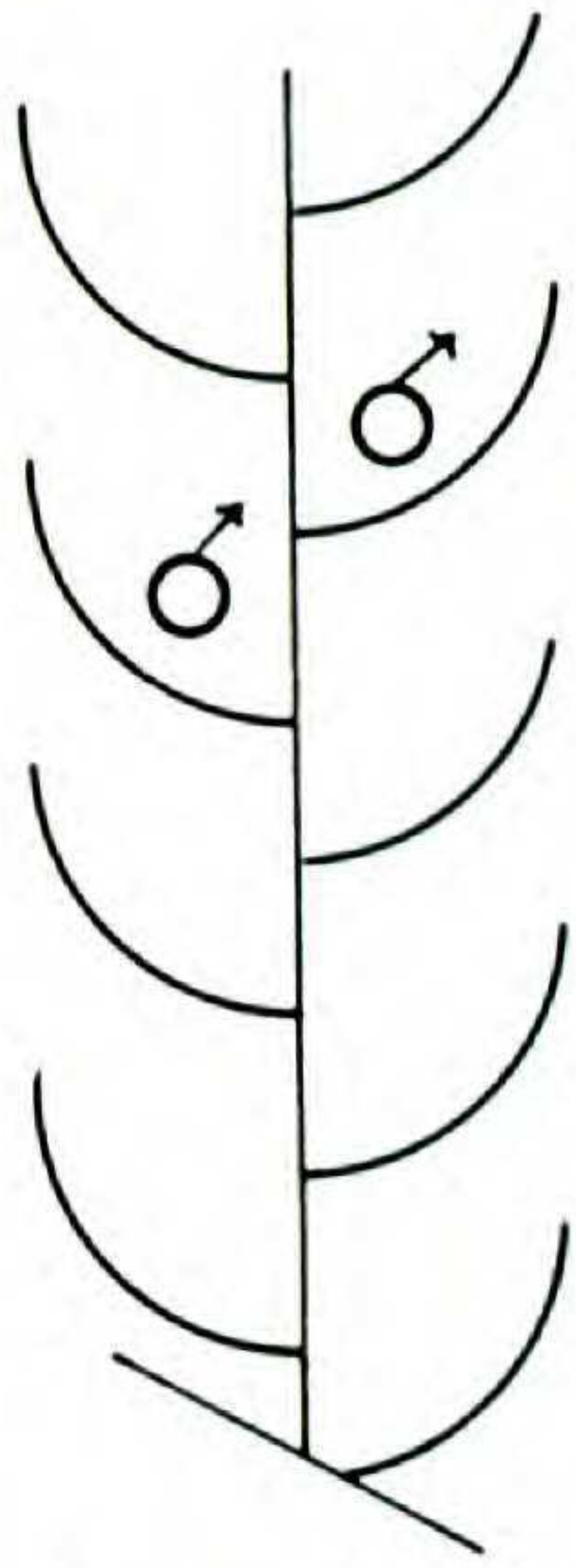
Since *Scleria* does not seem to have the same structure as the four genera of Group III, it cannot be combined with them in the same tribe. These four genera are distinct enough to be in a tribe of their own. The oldest name at a tribal level is Hoppieae Pax, 1886, based on the illegitimate *Hoppia* Nees, 1842, a later homonym of *Hoppia* Spreng., 1818 (Gentianaceae, = *Hoppea* Willd., 1801). Pax's Hoppieae, however, also included his subtribe Chrysitrichinae, i.e., the present tribe Mapanieae, so that my Group III really corresponds to Pax's subtribe Hoppinae. However, since a tribal name must be based on a legitimate generic name, the present tribe must then be called Bisboeckelerae Mattf. in Diels, 1936.



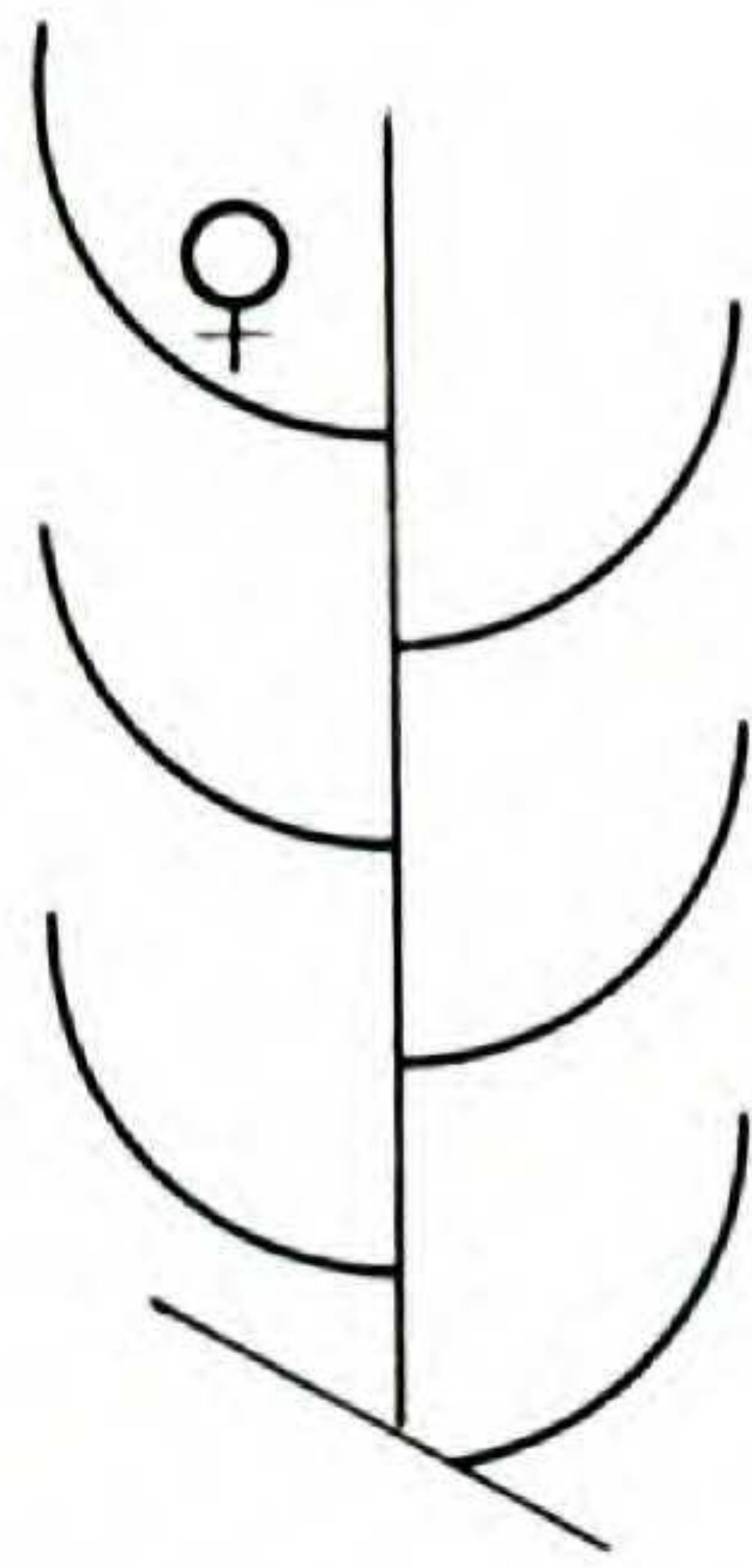
FIGURES 19–20. Branching patterns of “compound spikelets,” inflorescence units of genera of Group IV.—19. *Coleochloa*. This particular example is of an exceptional specimen in which the female true spikelets bear two female flowers, which are therefore lateral, instead of the usual one which is pseudoterminal, although generally considered terminal.—20. *Trilepis*. Left, male compound spikelet; right, female compound spikelet.

GROUP IV

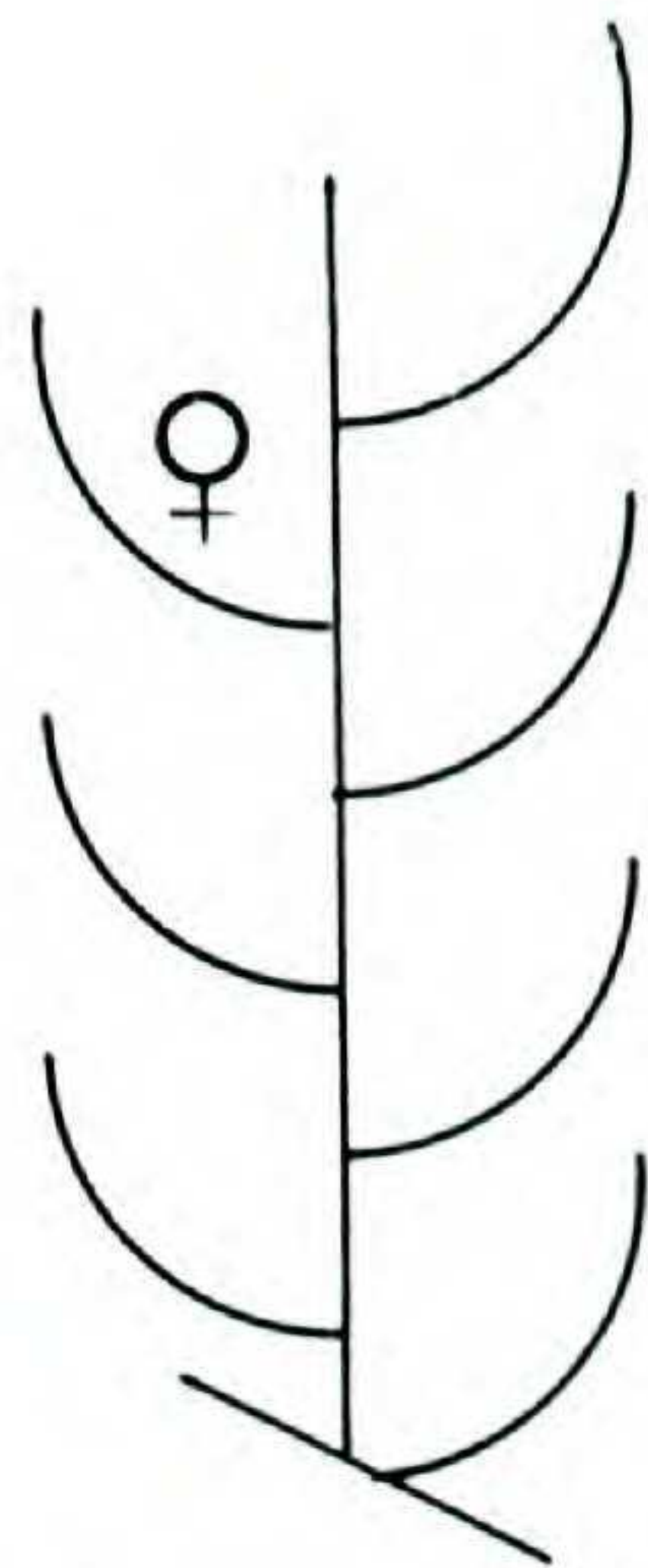
The inflorescence is formed of “compound spikelets.” These are the ultimate inflorescence units which can be externally delimited visually and resemble from the outside the true spikelets of Group I. The compound spikelet is composed of an axis which laterally bears few to many unisexual true spikelets (the “partial spikelets” of Koyama & Maguire, 1965). Each true spikelet arises in the axil of a glumiform covering bract; its rachilla bears one or more lateral flowers subtended by glumellas. Sometimes a prophyll is visible at the base. The “compound spikelet” is, then, really a panicle. It is unisexual in *Trilepis*, that is, all the true spikelets in the “compound spikelet” have flowers of the same sex (Fig. 20); in the inflorescence, the male compound spikelets are in the lower part and the female ones in the upper part. In **Coleochloa* the compound spikelet is bisexual, that is, the true spikelets at the base of the compound spikelet are male, while the true spikelets in the upper part of the compound spikelet are female (Fig. 19). Some of the true spikelets, at the apex or the base of the compound spikelet, have no flowers.



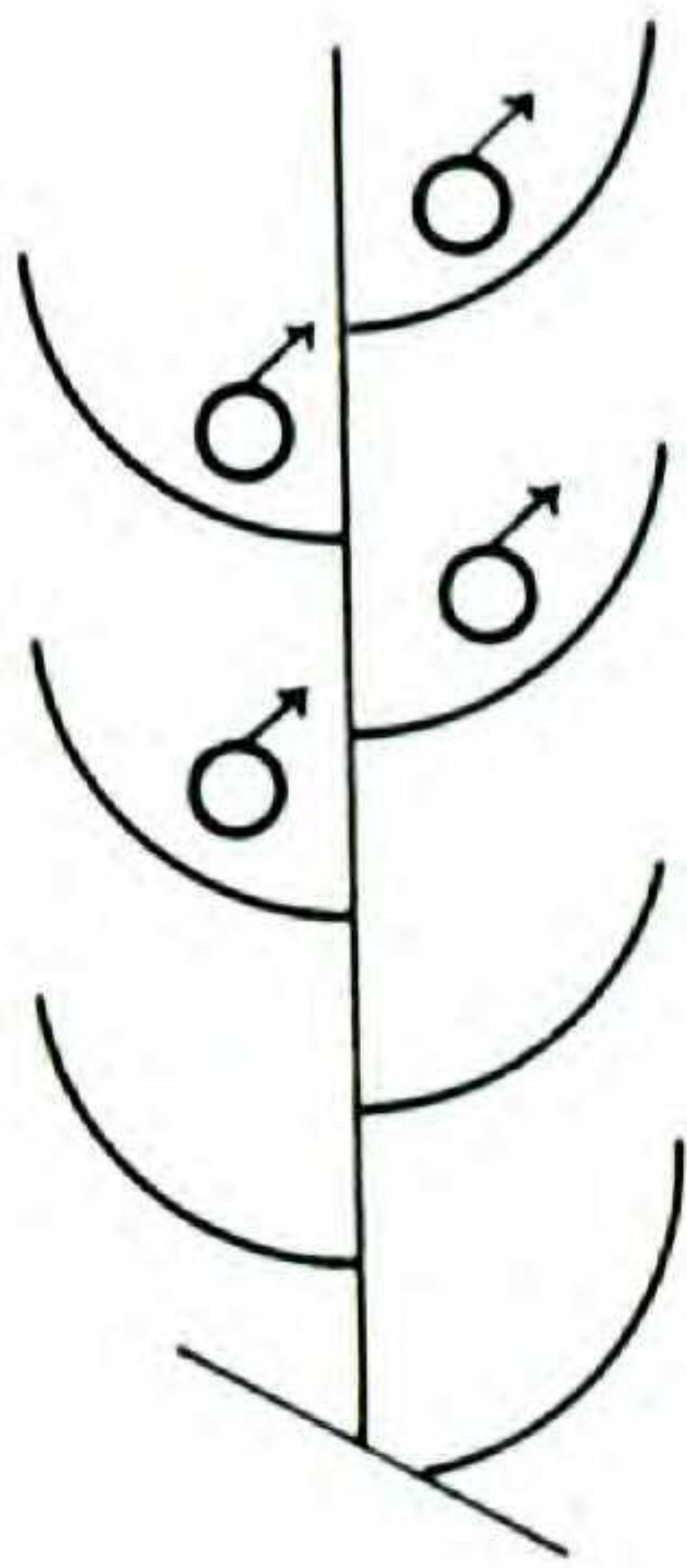
CEPHALOCARPUS



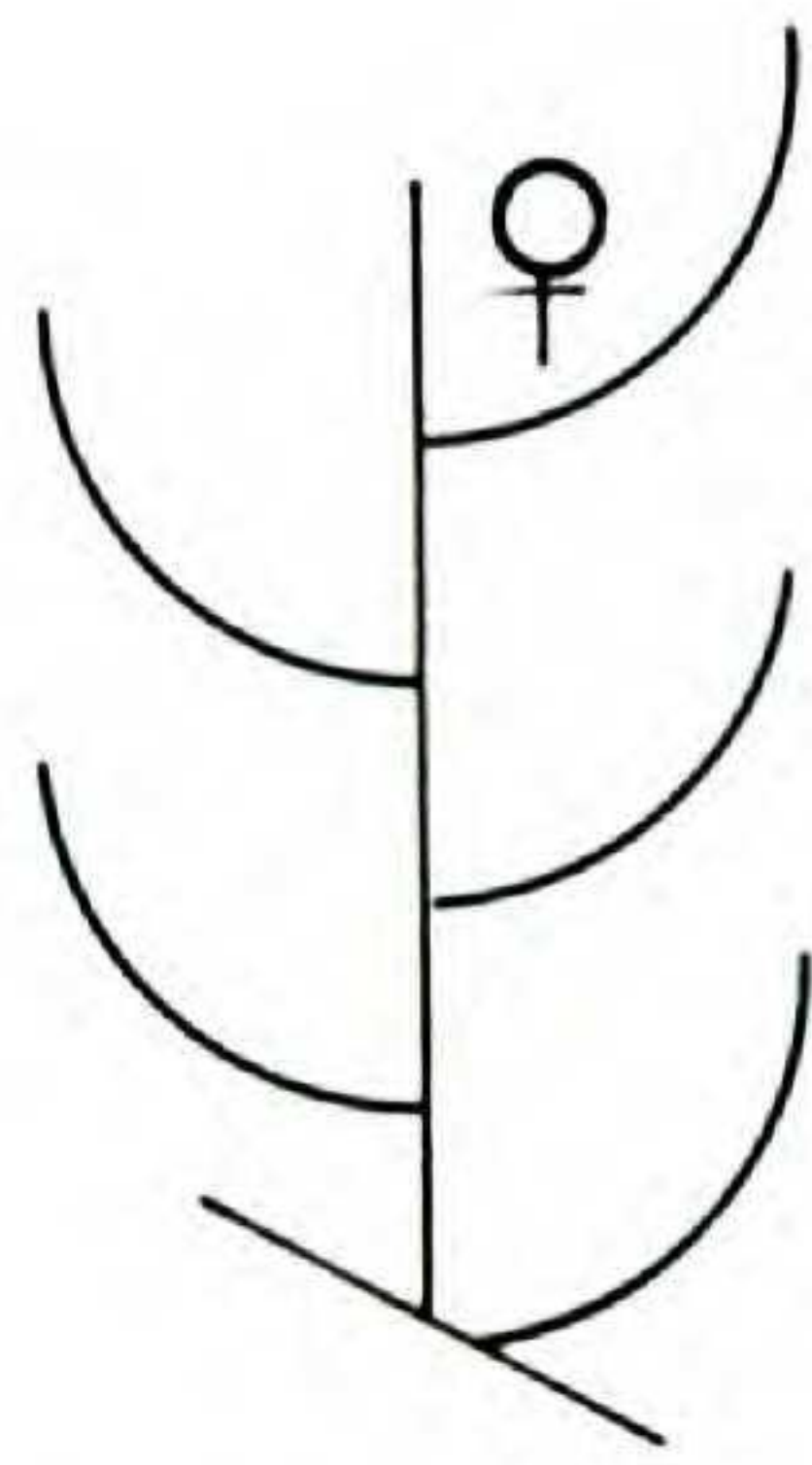
CEPHALOCARPUS



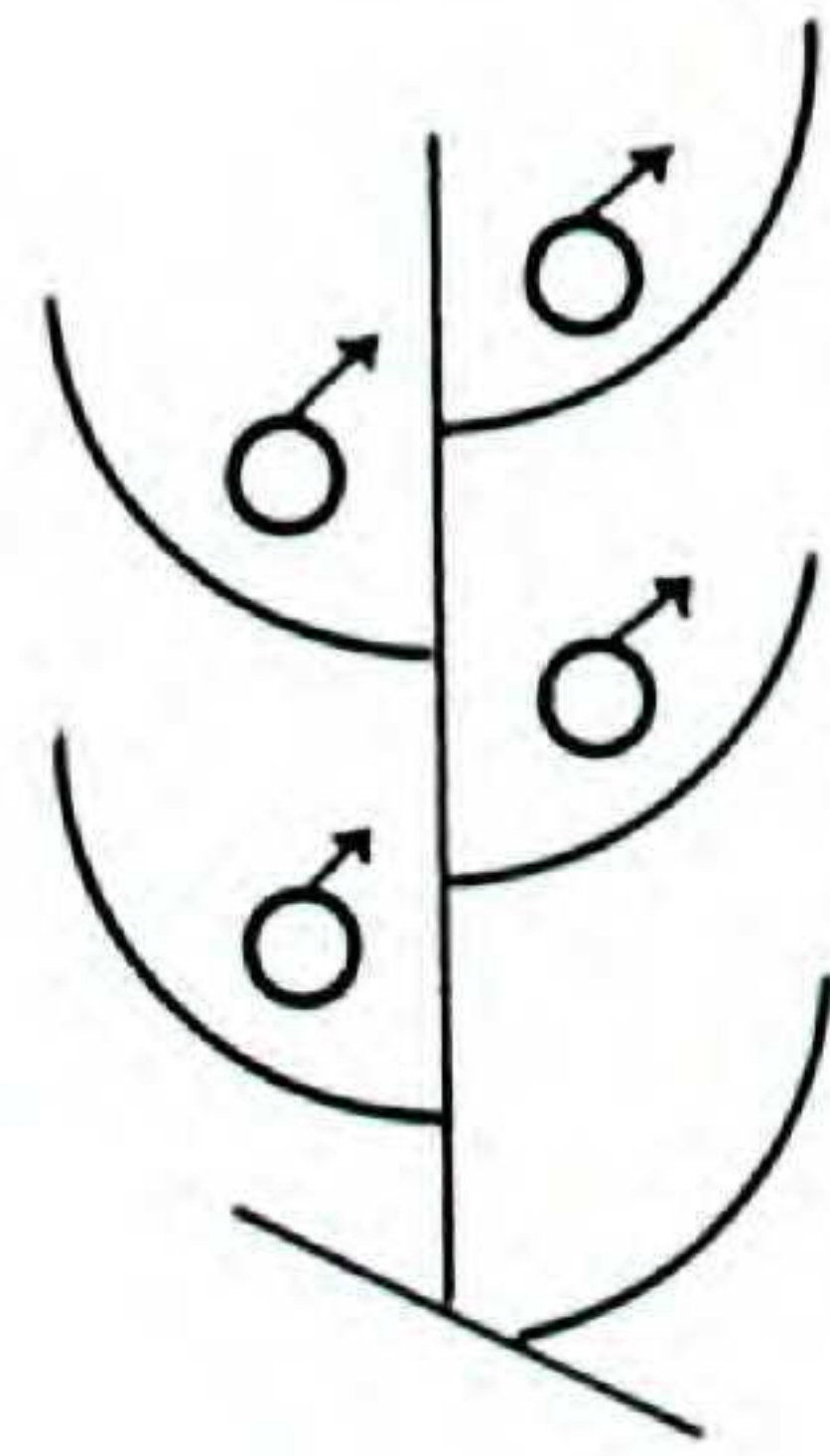
EVERARDIA



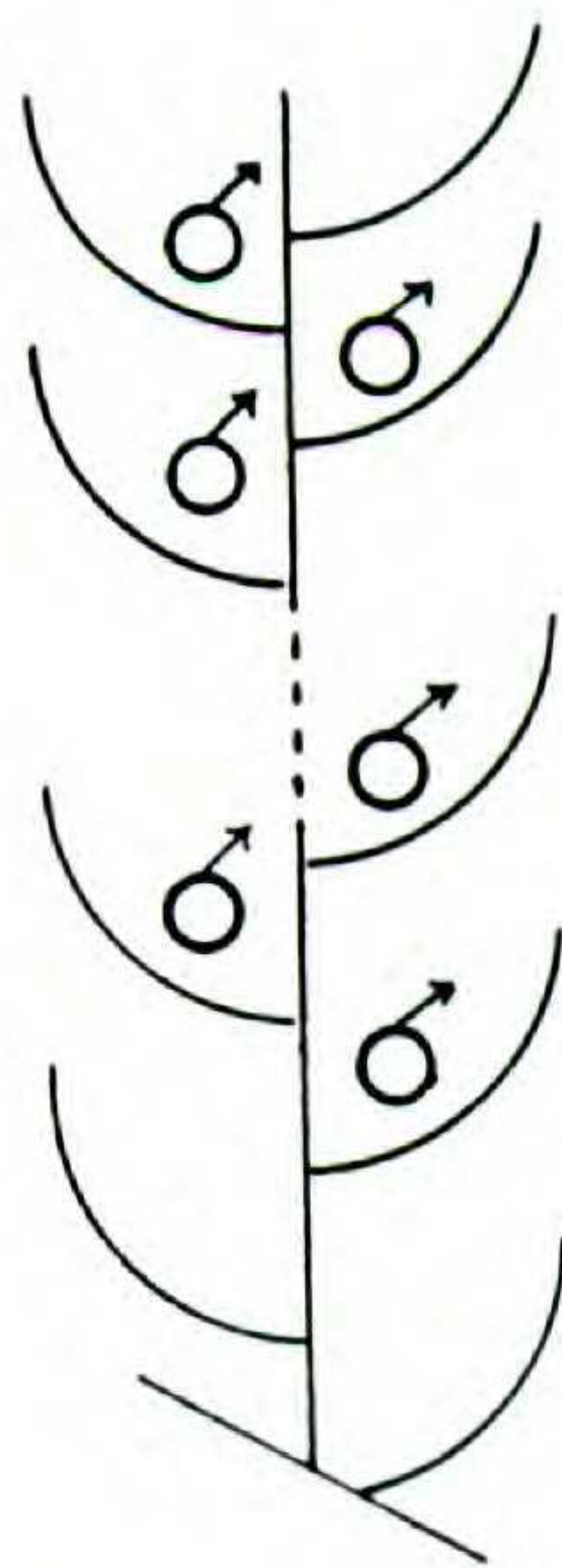
EXOCHOGYNE



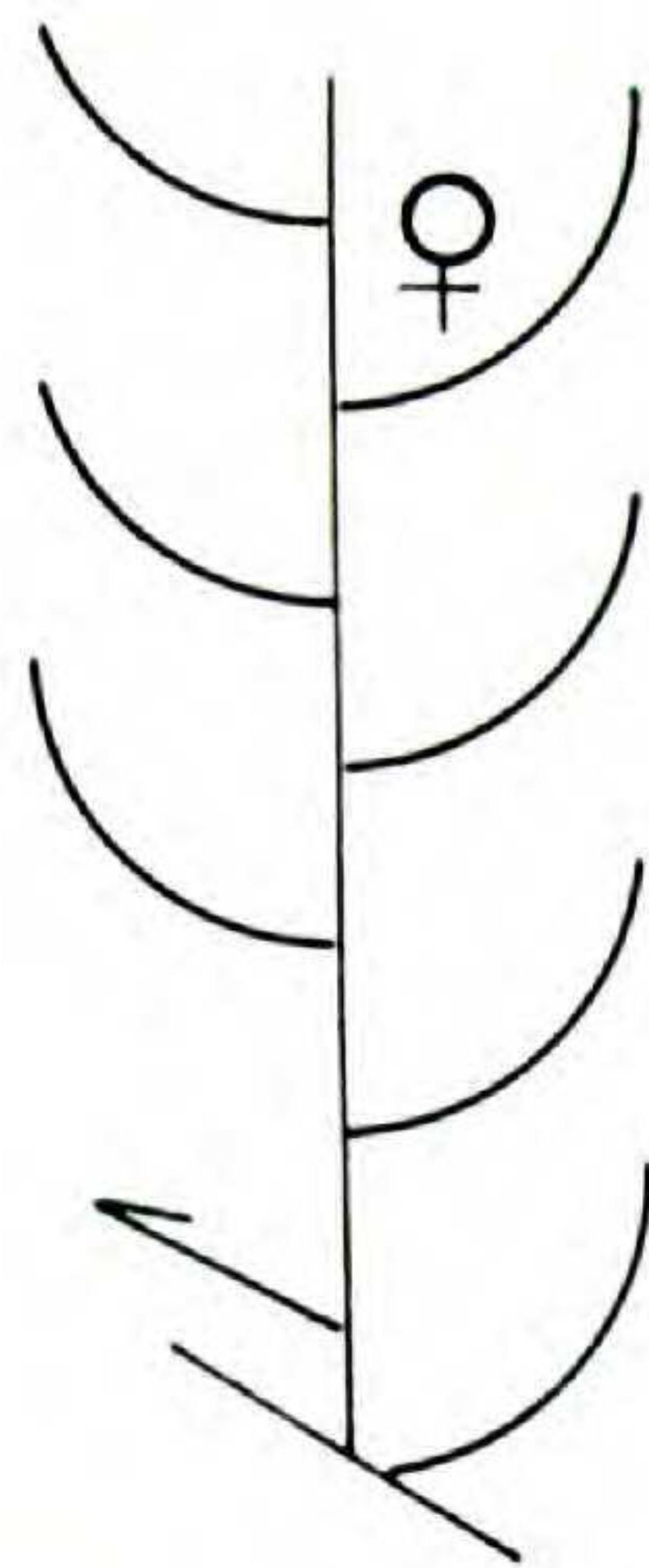
EXOCHOGYNE



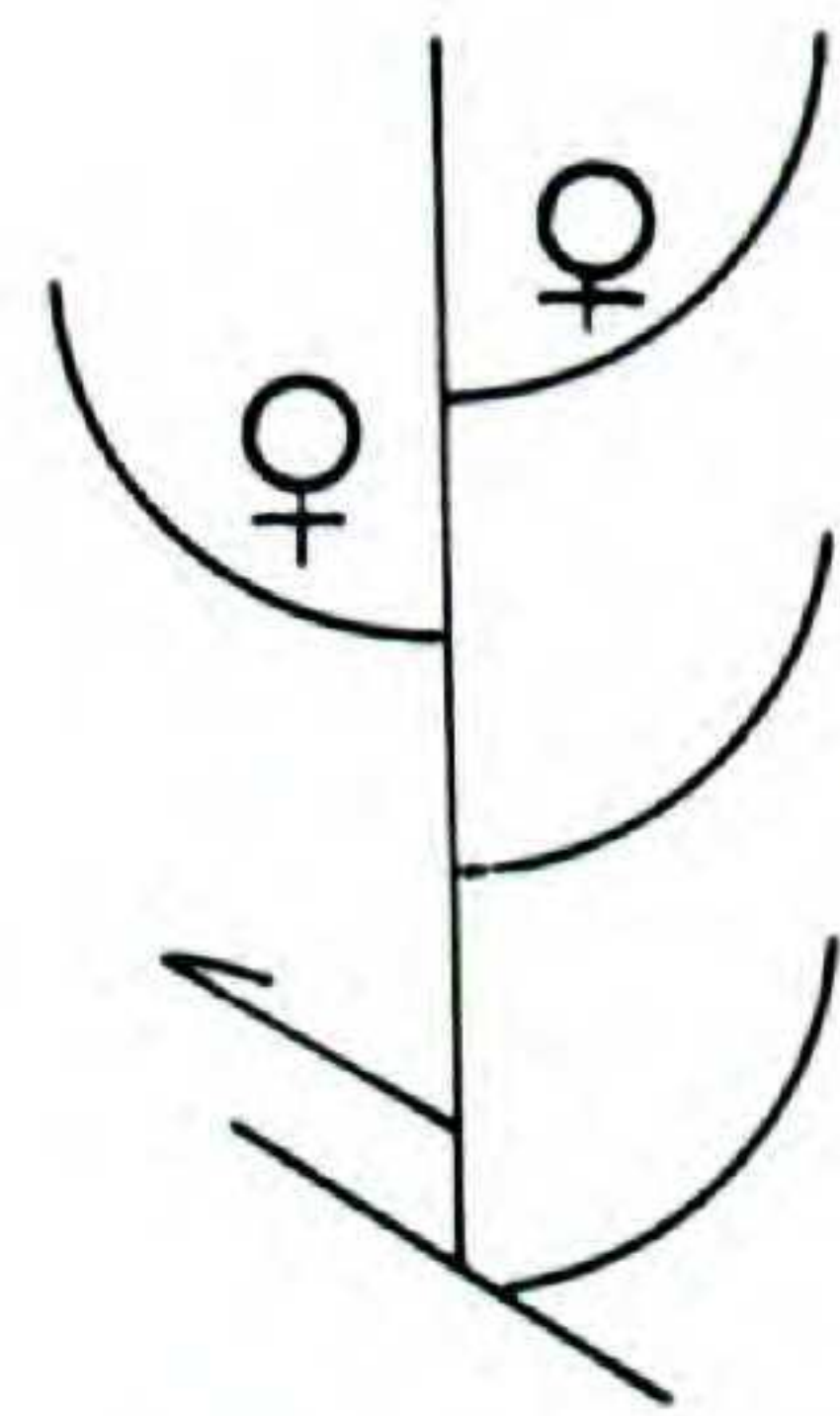
LAGENOCARPUS



LAGENOCARPUS



LAGENOCARPUS



LAGENOCARPUS

The ultimate inflorescence unit in this group is of two types: (1) "Compound spikelet" with the prophyll and subtending bract of its main axis if these laminas are immediately adjacent. (2) "Compound spikelet" without these laminas if they are not immediately adjacent but separated by other branches on that axis.

Two genera exemplify this group: **Coleochloa* and *Trilepis*.

Group IV contains those genera of the tribe Lagenocarpeae with "compound spikelets." Besides *Coleochloa* and *Trilepis*, it also includes the African genera, *Afrotrilepis* and *Microdracoides*. The female flowers of all the genera of this tribe are considered truly terminal by Pax (1886), Schultze-Motel (1964), Koyama & Maguire (1965), and Koyama (1969), but there exists evidence contrary to this view. The female spikelet is always described as having empty basal glumes and the terminal pistil as being enveloped in the most distal glume. But possibly the pistil arises in the axil of this distal glume and is therefore lateral, that is, "pseudoterminal." By the simple outward appearance one cannot distinguish between these two possibilities.

Examining a collection of *Coleochloa setifera* (Ridley) Gilly from Tanzania, Africa (*Richards 20007*, duplicate examined in my personal herbarium, other duplicate in K), I found that all its female true spikelets had *two* pistils at the apex of the rachilla, at almost the same level, both well developed and each subtended by a glume (Figs. 19, 36–37). Two pistils cannot both terminate the same axis. In some "compound spikelets" the upper female flower had no further organs above it, so the branching pattern would be like that shown in Fig. 19. In other "compound spikelets" there was a glume above the upper female flower, as shown in Fig. 36. The latter case is particularly strong evidence that both female flowers are lateral on the rachilla. Therefore, in this genus, even when there is one pistil, as from the literature there usually seems to be, it is lateral.

GROUP V

The inflorescence terminates in spikelets which are isolated or grouped in fascicles. These are true spikelets. The male spikelets possess basal empty glumes and few to many distal lateral staminate flowers. The female spikelets have several basal glumes and what is usually considered a terminal pistil (Fig. 21).

This group is exemplified by: *Lagenocarpus* (including *Cryptangium*), *Cephalocarpus*, **Everardia*, **Didymiandrum*, and **Exochogyne*.

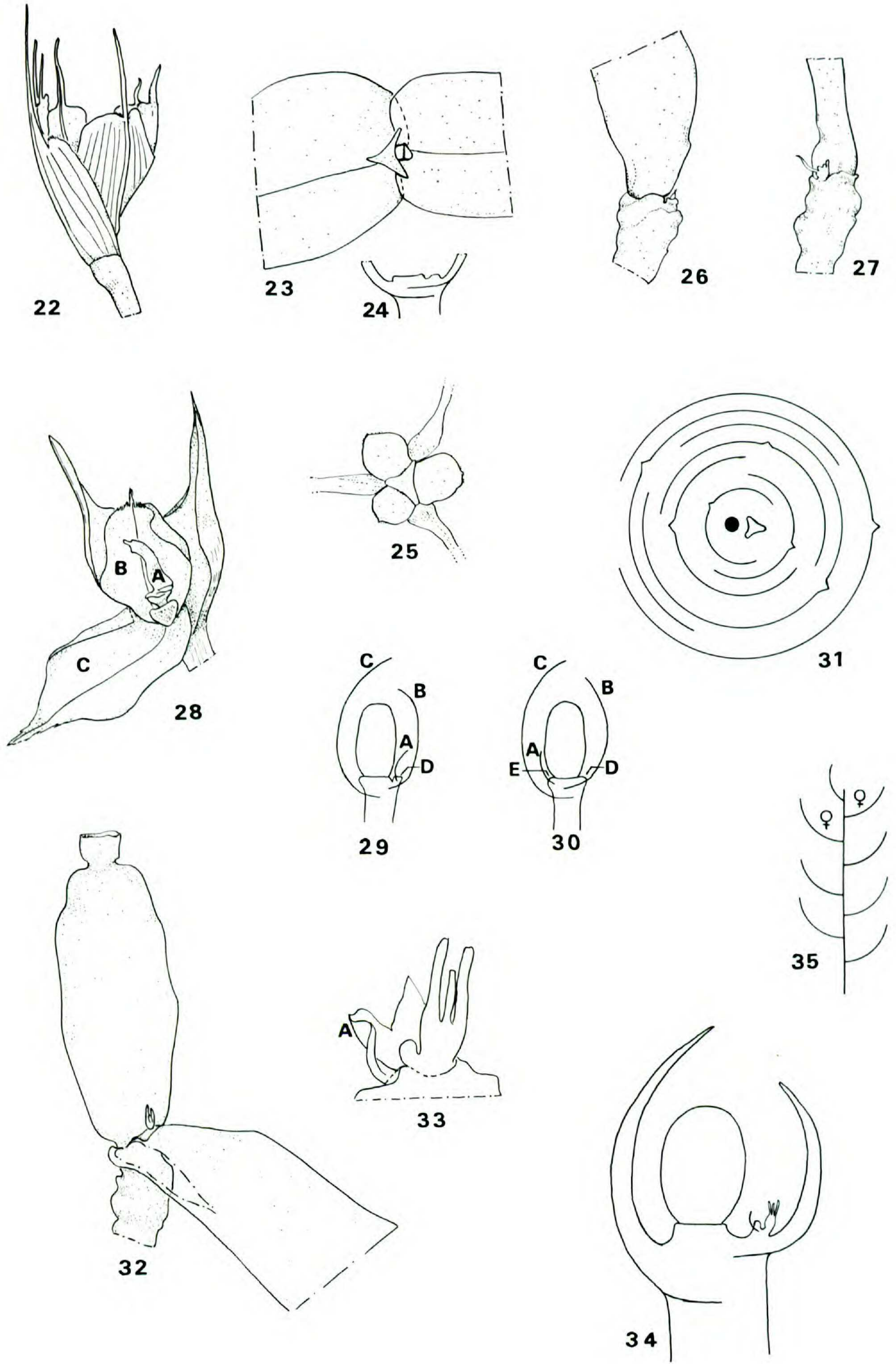
The genera of this group are those of the tribe Lagenocarpeae which do not have "compound spikelets" but only true spikelets.

The ultimate inflorescence unit in this group is the male or female spikelet plus the prophyll (when present) and subtending bract of the rachilla axis.

The branching pattern of the ultimate inflorescence units of this group differs from that of Group I only if the pistil really is terminal, which is the general

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FIGURE 21. Branching patterns of inflorescence units of genera of Group V. Note variation in number of glumes and flowers in the same genus and that the prophyll is not always present. In Figs. 19–21 the apical pistil is shown as a lateral (pseudoterminal) female flower, in accord with the position adopted in this paper, rather than as a terminal flower.

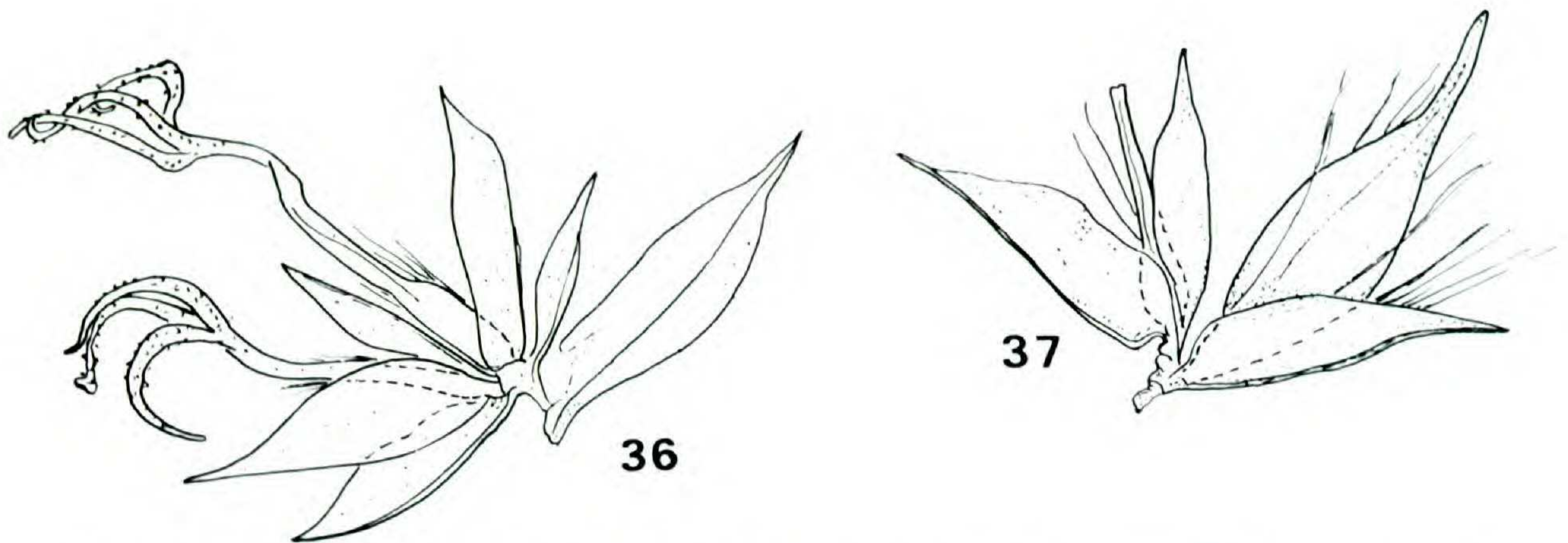


opinion of cyperologists. But there is doubt in this respect. Observations I have made show that the female flower is really lateral. In a collection of *Everardia surinamensis* Gilly, (*Maguire et al.* 53714, Venezuela, det. Koyama, duplicate in UB examined, other duplicates occur in NY and other herbaria), the pistil at the apex of the female spikelet was observed to be subtended by the penultimate distal glume. The rachilla continued beyond the base of the fruit, bearing a well reduced ultimate glume. The pistil in this collection, then, was clearly lateral in the axil of the penultimate glume.

A similar series of observations was made in *Lagenocarpus rigidus* Nees (subsp. *rigidus*, *Irwin et al.* 12995, Brazil, near Brasília, det. Koyama, [UB]; subsp. *tenuifolia* (Boeck.) Koyama & Maguire, *Brade* 13522, Brazil, Minas Gerais, Diamantina, det. Koyama, [RB]). Several constructions were noted at the apex of the female spikelets. They all have several large glumes below an apparently terminal female flower or fruit (Fig. 22). However, careful examination of the rachilla tip

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FIGURES 22–35. Views of parts of female spikelets of *Lagenocarpus rigidus* Nees.—22. Cupule of glumes of a female spikelet, the mature fruit having been pulled out; *Brade* 13522; $\times 6.5$ —23. View of base of the interior of this cupule showing the penultimate glume on left, ultimate (most distal) glume on right, the raised triangular scar left by the fruit, at its right a depressed rectangular area representing part of the distal surface of the rachilla, and at its right a small triangular area of raised tissue representing the apex of the rachilla; $\times 18$.—24. Diagram showing profile of the surface shown in Fig. 23.—25. View of base of the fruit which was pulled out of this cupule of glumes, showing scar, 3 grooves, and 3 hypogynous squamellae.—26–27. Distal part of rachilla and base of fruit showing, respectively, side and dorsal views of rachilla apex at the side of the base of the fruit; *Irwin et al.* 12995; $\times 22$. In Fig. 27 the thin extension to the left from the parenchymatous rachilla point represents a very small vestigial glume.—28. Cupule of glumes with lower glumes and fruit removed and front (penultimate large) glume, C, pulled down to show fruit scar and vestigial glume, A; $\times 6$. The vestigial glume is wrinkled in its basal portion and has been pressed by the fruit against the ultimate large glume, B. (A single short length of vein, not demarked here, occurs on the right side of the vestigial glume about midway between its base and tip.)—29. Diagram interpreting the two possibilities of the construction shown in Fig. 28. See text for discussion.—30. Diagram showing possible interpretations in the hypothetical case of the vestigial glume, A, being on the opposite side of the fruit from the ultimate large glume, B. This construction was *not* seen in the material examined. Here, there would be three indistinguishable possibilities: (1) The fruit is in the axil of the ultimate large glume, B, and the apex of the rachilla is on the opposite side at E. (2) The fruit is in the axil of the vestigial glume, A, and the apex of the rachilla is on the opposite side at D. (3) The fruit is terminal.—31. Cross-sectional diagram of a female spikelet examined (that shown in Fig. 22) showing fruit scar, position of rachilla apex (dark spot next to scar) and the glumes. The absolute size of the glumes is not indicated but the position of the midvein of each and the proportion of the circle it covers near its base is accurately shown. This spikelet was representative in its phyllotaxy of several examined.—32. Distal portion of rachilla, ultimate large glume (torn at base) and fruit of a female spikelet. The other glumes were removed. At the base of the fruit can be seen a vestigial pistil (shown magnified in the following figure); *Irwin et al.* 12995; $\times 22$.—33. Vestigial pistil of Fig. 32, showing the three styles, and on its left side a small spherical projection of tissue which is the apex of the rachilla; $\times 56$. Back of the pistil is a vestigial glume (its base torn from its connection around the front of the pistil and pushed back). Its single vein is along its fold at A. It is not clear whether the large notch at the far side of the glume is natural or a result of tearing during preparation.—34. Diagram showing placement of the organs at the distal end of the rachilla of the female spikelet of Fig. 32.—35. Branching pattern of this complete spikelet, showing the number of glumes actually found in it. Since the axis of this spikelet bore other organs below, its prophyll and subtending bract were not next to the spikelet.



FIGURES 36–37. True spikelets of *Coleochloa setifera* (Ridley) Gilly with two female flowers each; Richards 20007; $\times 13.5$.—36. The subtending bract of the true spikelet is shown, partially detached, at right, the two lower empty glumes, and the two upper glumes, each with a pistil.—37. In this spikelet, the subtending bract is not shown and the pistils are at an earlier stage of maturity. The lower pistil is covered by its glume but the long ovary hairs are visible.

around the base of the fruit showed a small raised point of tissue that is the apex of the rachilla (Figs. 23–24), or the apex with a projection interpreted as a vestigial glume (Figs. 26–27). In both cases the fruit appeared to be in the axil of the *penultimate* large glume; this is particularly evident in Fig. 23. When the raised point is the rachilla apex alone, the branching pattern would be as in Fig. 21, bottom row, middle. It should be emphasized that the small bits of tissue referred to are *not* the hypogynous squamellae at the base of the fruit. Figure 25 shows a basal view of the fruit that was pulled out of the cupule of glumes whose inside is shown in Fig. 23. All the squamellae went with the fruit but the raised bit of tissue referred to is still in the cupule and separate from the scar left by the fruit (Figs. 23–24). In another case the raised rachilla apex grew concrescent to the base of the ultimate large glume, appearing as an outgrowth on its base rather than separate as in the previous case.

Another construction is shown in Fig. 28. Here, a much better-developed vestigial glume, A, arises from the rachilla tip on the *same* side of the fruit as the next lower and larger glume, B. The central axis of both the vestigial and the adjacent large glume are on neighboring radii. This can only be interpreted as in Fig. 29, and it allows two possibilities: (1) The fruit is lateral and in the axil of the penultimate large glume, C. (2) The fruit is terminal on the thick rachilla and glumes B and A are borne on a new side branch (D) arising from that rachilla just below the fruit. The latter interpretation is similar to Koyama's present view of *Scleria*. As in *Scleria*, there is no direct evidence for the existence of a new branch since the vestigial glume does not have the aspect of a prophyll. Since the latter interpretation is the more complicated of the two, it should not be accepted without further evidence. The simpler interpretation that the axis is unbranched and the fruit is lateral is preferred. For if the fruit were terminal on an unbranched rachilla, then the vestigial glume (when there is one) would have to be on or near to the *opposite* side of the fruit from the uppermost large glume, such as is represented in Fig. 30. This is because the phyllotaxy of the glumes in a female spikelet, although not regular, is such that successive glumes are not

next to each other (that is, on radii forming small acute angles) but are on radii about 100° – 180° apart (Fig. 31). The vestigial glume being on the side of the fruit opposite from the uppermost large glume is a necessary, but not the sole, condition for the fruit to be interpreted as terminal, for two other interpretations are also consonant with this position, namely, that the fruit is lateral and in the axil of the uppermost large glume, or, less likely, that the fruit is lateral and in the axil of the vestigial glume.

In another case, two vestigial glumes around a raised rachilla apex at the side of the base of the fruit was observed.

Another and rarer construction is the presence of a second and more distal pistil at the rachilla tip. This was noted several times. In one case the second pistil was relatively large but no other part was noted distally to it. In this case the interpretation of the spikelet would be like that indicated in Fig. 21, bottom row, right, that is, both pistils are lateral on the same axis. It is true that one could argue that the lower pistil is terminal on the main rachilla and the second pistil terminal on a side branch even though there is no independent evidence for such a branch. But this argument would not hold for the case illustrated in Figs. 32–34. Here, besides the vestigial second pistil in the axil of the ultimate large glume (the lower pistil, now a fruit, being in the axil of the penultimate large glume), there is a vestigial glume distal to the vestigial pistil, as well as a clearly visible rachilla apex. This arrangement certainly shows that the second pistil is lateral. Therefore, unless one is prepared to argue that the first pistil is terminal and the second is lateral, a very complicated hypothesis for which there is no independent evidence and which is contrary to all rules of morphology in the Cyperaceae, one must recognize that both pistils are lateral on a single axis, as diagrammed in Fig. 35.

The genera of Group V have not been placed in Group I because the lateral nature of the pistil has not yet been proved for all its genera but mostly because the flowers are all unisexual.

The evidence that in certain collections in several genera of the Lagenocarpeae the female flower is lateral, as well as the probable lateral nature of the female flower in *Scleria*, shows up a certain weakness in Koyama's definition of the subfamily Mapanioideae (1967, 1969, 1971)⁴ defined as having terminal female

⁴ Koyama calls the fruit in this subfamily a "fructification" because it consists of more than the mature ovary. However, there is no necessity for a new term. In other families of the angiosperms a fruitlike structure incorporating other parts besides the mature ovary has always been called a "simple accessory fruit." He calls the external tissue surrounding the pericarp a "utricle." This term is not well chosen since utricle means "bladder," that is, a structure which is inflated, with a rather large space around what it surrounds and with the outer wall rather soft or flexible. In no cyperaceous fruit is the outer tissue flexible at maturity, and in several of his examples the space between the outer wall and the pericarp is filled with parenchymatous tissue, so it is no bladder at all. Thus Koyama (1971: 606) states that in Lagenocarpeae other than *Trilepis*, *Coleochloa*, *Afrotrilepis*, and *Microdracoides*, "the utricles cannot be readily recognizable since the utricles are so completely adnated to the achene pericarp that no superficial distinction can be made between the two organs (Figs. 5 & 8)." There must be some mistake in the figure reference since his Figs. 5 (*Lagenocarpus*) and 8 (*Hypolytrum*, which, by the way, is not a Lagenocarpeae) show sections of fruits in which the outer wall and the pericarp are very distinct. In the 1969 paper they are also distinct for the same two genera in his Figs. 39, 40.

flowers and including the tribes Sclerieae (including Bisboeckelereae), Lagencarpeae, and Mapanieae.

GROUP VI

The inflorescence is composed of one or more spikelike structures on a culm. Kükenthal (1909) calls each of these a "spicula propria" or simply "spicula." When there is only one, its axis is the tip of the culm itself. In *Schoenoxiphium* and *Kobresia* (Fig. 38A) the spikelike structure is made up of a rachis basally bearing lateral bisexual spikelets ("partial inflorescences") and, apically on the same rachis axis, lateral male flowers. Both the spikelets and male flowers are subtended by glumelike bracts. (The male flowers on the rachis are absent in one species of *Kobresia*.) The spikelike structure, therefore, is technically not a spike although it is often called such, but rather a condensed spikelike panicle. Each lateral bisexual spikelet has a rachilla with a single basal lateral female flower in the axil of a clasping enrolled lamina, generally considered a prophyll, whose lateral margins are fused below, and several apical lateral male flowers in the axils of glumes. The rachilla is a thick, long, visible structure in *Schoenoxiphium*, or a thin, very short, almost invisible structure in *Kobresia*. The male flowers in the spikelets may be reduced to one or be absent; this is rare in *Schoenoxiphium* but common in *Kobresia*. When all the male flowers in a spikelet are absent, the bisexual spikelet becomes female by reduction. Kükenthal calls each of these lateral spikelets which bears a pistil a "spicula partialis" but he also applies the same term to the apical portion of the spikelike structure that bears male flowers directly on its own rachis. This is confusing because these two positions for male flowers are on axes of different branch orders.

In *Uncinia* (Fig. 38B) the spikelike structure is the same, with apical male flowers and basal lateral spikelets. In this genus, however, the lateral spikelets are always purely female, never bearing male flowers. The rachilla extends beyond the orifice of the utricular lamina (perigynium, generally considered a prophyll) and is provided with a hook made by a transformed glume (Snell, 1936; Mora Osejo, 1966), or in one species by the tip of the rachilla itself (Kukkonen, 1967). The hook is used for disseminating the fruit by sticking to the feathers of birds or the fur of mammals.

In *Carex* (Figs. 38C–38H) the spikelike structure has several patterns of flower arrangement. Its axis (rachis) bears lateral male flowers directly and female spikelets laterally, both in the axils of glumelike bracts. The female spikelets may be all grouped together (1) along the basal portion of the spikelike structure (in which case the structure is called "androgynous," or by Kükenthal, "hypogyna"), (2) along the apical portion ("gynaecandrous" or "acrogyna"), (3) in the middle portion with male flowers above and below ("mesogyna"), (4) on both the apical and basal portions with male flowers in the middle ("mesandra"), or (5) the female spikelets may be intermixed singly and alternately along the spikelike structure with male flowers ("alternans"), finally, (6) the male flowers may be on separate spikelike structures from the fertile spikelets ("unisexual," the species usually monoecious, rarely dioecious). The rachilla of the female spikelet bears a single lateral female flower (pistil) in the axil of a utricular

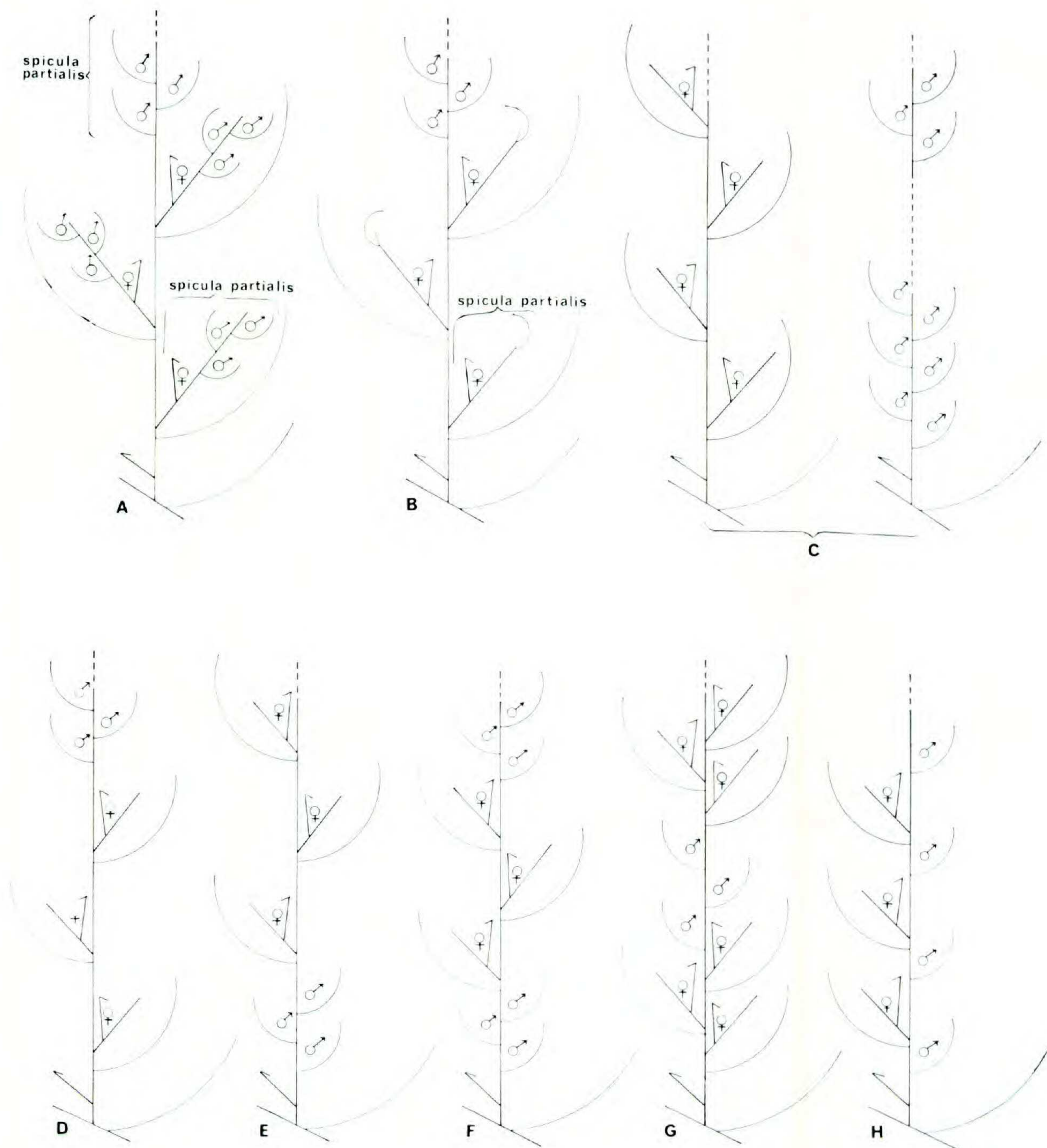


FIGURE 38. Branching patterns of the spikelike structures ("spiculae propriae") in genera of Group VI. The male flowers on the central rachis together form a single "spicula partialis," and each lateral bisexual or female spikelet is also a "spicula partialis," in the terminology of Kükenthal. The number of male flowers and of spikelets on a rachis, as well as the number of male flowers on the rachilla of a bisexual spikelet, varies among different species, individuals and spikelets. A conventional number of these units is shown here.—A. *Schoenoxiphium* and *Kobresia*.—B. *Uncinia*.—C–H. *Carex*.—C. Unisexual.—D. Androgynous or hypogynous.—E. Gynaecandrous or acrogynous.—F. Mesogynous.—G. Mesandrous.—H. Alternate.

lamina (perigynium, generally considered a prophyll). In one species, *C. sitchensis* Prescott ex Bong., as a usual feature (Clarke, 1909; Kükenthal, 1909), and in other species occasionally as teratological events, the rachilla may be prolonged beyond the base of the pistil and bear glumes and a male flower. In a few species the rachilla may be more or less prolonged beyond the base of the pistil although not bearing glumes or male flowers (especially *C. microglochis*

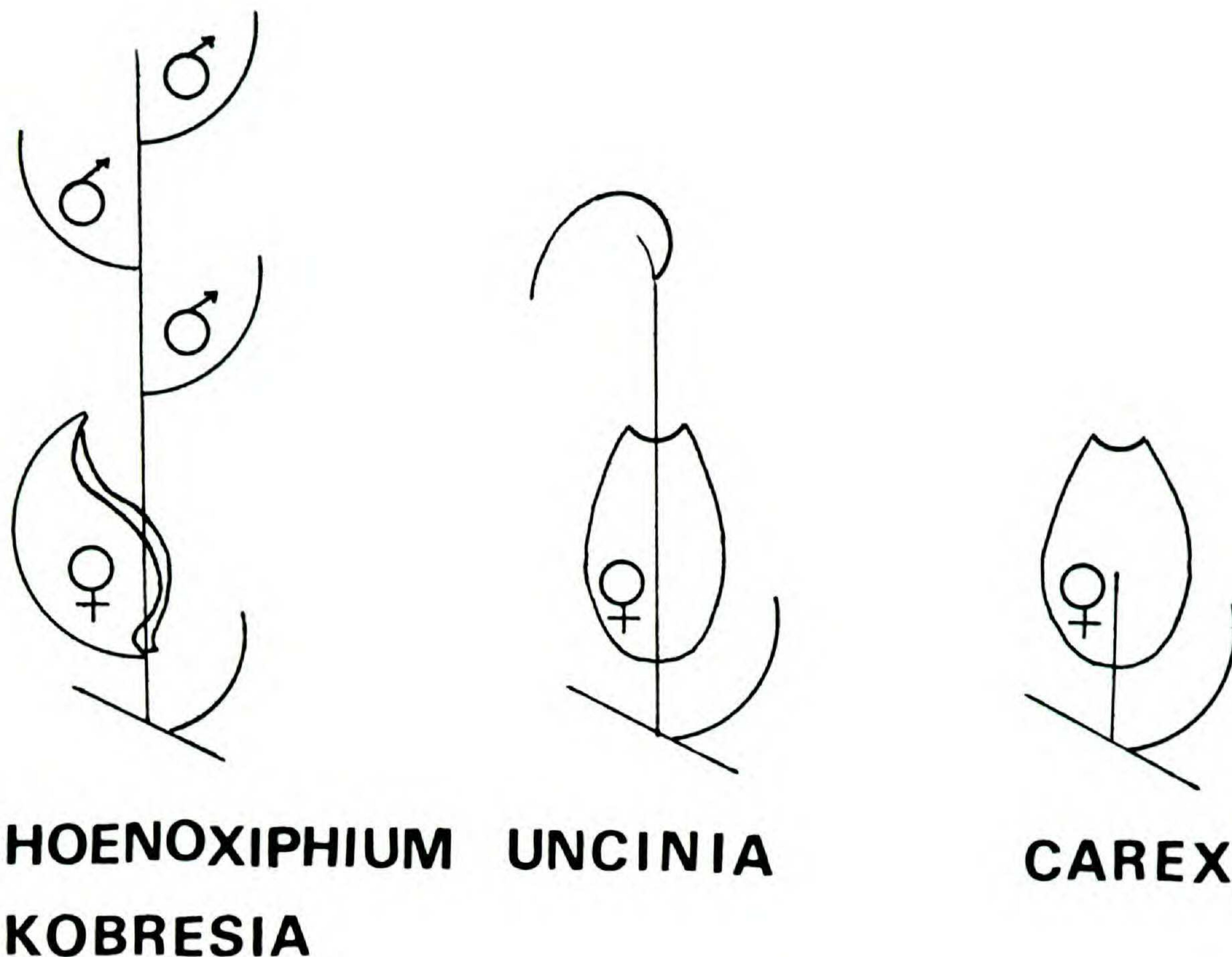


FIGURE 39. Branching patterns of the pistil-bearing spikelet of genera of Group VI. The female flower is apparently in the axil of a lamina (generally considered a prophyll) which is partially (*Schoenoxiphium* and *Kobresia*) or completely (*Uncinia* and *Carex*) transformed into a utricle.

Wahlenb. where it is exerted from the orifice of the perigynium). In the vast majority of species of *Carex* the rachilla is not prolonged so that the pistil appears to be terminal on it.

Thus, among the four genera, the spikelet containing the pistil forms a somewhat uneven reduction series from *Schoenoxiphium* to *Carex* (Fig. 39).

The assumption that the basal clasping or utricular lamina on the female flower-bearing rachilla is really a prophyll, and that the female flower is really borne in its axil, makes the Cariceae different from all other tribes of the Cyperaceae. For in no other tribe does a prophyll of the rachilla axis, occurring immediately below a true spikelet, bear a flower or indeed any axis at all in its axil. (I consider the two basal, lateral, folded, keeled laminae in the Mapanieae pseudanthium, which in most genera bear male flowers of one stamen in their axils, to be glumes, not prophylls. Paired, opposite, lateral prophylls are typical of the dicots, but do not occur otherwise in the Cyperaceae, and, in fact, are extremely rare in the monocots in general; the only example I know of is in *Dioscorea* (Arber, 1925: 132, fig. civ, 4), where they may more properly be said to be subopposite, and do not bear flowers in their axils.) Therefore, it is necessary to make an exception for the Cariceae and consider the prophyll in this tribe

to be part of the spikelet. So far, neither of the above two assumptions can be excluded, but the subject should be studied further to see if they are indeed true.

Two kinds of ultimate inflorescence unit are defined for Group VI: (1) The female flower-bearing rachilla with its distal male flowers, if any, and with its basal clasping or utricular prophyll, plus the subtending bract of the rachilla. (2) Each single male flower on the rachis of the spike (when this occurs) plus its subtending bract.

Kukkonen (1967) believes that in *Uncinia* the stipe below the pistil bears the pistil terminally and that the continuation of the rachilla is a new branch, that is, the stipe plus the branch that forms the hook is a sympodial axis. Therefore, the perigynium is not the prophyll bearing a lateral pistil in its axil but the subtending bract of the new branch. If this were true for *Uncinia*, it would probably be true for the rest of the Cariceae also. However, the only evidence he gives for this contention is the fact that the central vascular strand (several bundles pressed together) in the stipe below the pistil is thick and goes in a straight line to the pistil, while the two (or in *U. kingii* Boott, one) vascular strands that go to the continuation of the rachilla are thin traces that diverge laterally from the thick central strand. This, however, proves nothing about which of the two branches (that to the continuation of the rachilla and that to the pistil) is the true continuation of the basal part of the thick strand and which is a new branch, since the branching pattern in the two cases is topologically the same. The thickness of a vascular strand is related to the size and rapidity of growth of the organ it supplies, and its orientation (straight or eventually bent) depends on the relative position of the organ it supplies as this is affected by compression or by the necessity of an organ to be in a particular position for functioning, etc. In primitive vascular plants with protosteles and siphonosteles in the stem, a new branch can usually be told from the continuation of the old axis by the pattern of vascularization alone, but this is not always possible in dictyosteles and, by the usual methods of investigation, is impossible to distinguish in the so differently vascularized monocot shoots, particularly in the graminoids, which are highly specialized monocots. It is impossible in the present case to make the distinction in these highly reduced ultimate inflorescence units of graminoids. Proof in this case must be based on prophylls when they exist, or on the branching pattern in lower orders of the inflorescence and the vegetative part of the plant where axes are thicker, internodes are longer, and leaf laminae are larger and more characteristic of what they really are.⁵

⁵ Anatomy is no help in this case when the usual methods of investigation are employed. Large monocots have thousands or tens of thousands of vascular bundles at any one level in a stem. Using an elaborate set-up of a specially constructed microtome and movie cameras, Tomlinson (1970) and Zimmermann & Tomlinson (1972, see bibliography for their earlier detailed papers) followed many individual bundles for long distances in the stem and traced their branchings and connections. By this analysis, one can tell a stem branch from a continuation of the old stem axis. However, to be of use in cyperaceous spikelets, a similar investigation would have to be made of the vascular pattern and connections of single bundles in the culms and then in the rachillas to see if the vascular patterns of stems and branches of the large monocots are preserved in these more highly reduced and modified structures. Only if they are could anatomy distinguish a monopodial rachilla from a sympodial pseudorachilla.

Group VI is exemplified by: **Schoenoxiphium*, **Kobresia* (including *Elyna*, *Hemicarex*), *Uncinia*, and *Carex*.

The genera of this group belong to the tribe Cariceae.

CONCLUSIONS

In this paper, entities at three levels have been discussed: (1) the *actual branching patterns* and sex of flowers in sedge inflorescences, of which examples of the last few branch orders are given or referred to; (2) the *definition* of "ultimate inflorescence unit" for the several cases; and (3) the *definition* of "spikelet." An ultimate inflorescence unit may be made up of a single spikelet, or of one or more spikelets plus other axes and laminas, or of a structure not yet considered to be a spikelet (as defined here) because its apparently terminal pistil has not yet been proved to be lateral. For these reasons it has been necessary to distinguish "ultimate inflorescence unit" from "spikelet" and to erect classes of the former as an aid in making subdivisions of the family.

The inflorescence patterns, along with other characteristics, allow grouping of the genera into tribes. The family may be divided into tribes directly or, if there seems to be a natural grouping of tribes, into subfamilies first. I believe subfamilies are possible and offer the following scheme with included tribes (plus *Dulichium* and *Scleria* whose tribal position is still uncertain).

1. Cyperoideae (= Rhynchosporoideae)

True bisexual flowers arranged in true, racemosely-branched spikelets. In the Rhynchosporoideae as a regular feature and sometimes in the other tribes, one or more flowers in a spikelet are male. Tribes Scirpeae, Cypereae, Rhynchosporoideae, and *Dulichium*.

2. Caricoideae

True, always unisexual flowers in true, racemosely-branched spikelets. Tribes Lagenocarpeae, Bisboeckelereae, Cariceae, and *Scleria*.

3. Mapanioideae

Flowers always unisexual, male flowers always with only 1 stamen; female flowers each joined with 2 or more male flowers to form a pseudanthium; rarely (*Syntrinema*) the female flower of a pseudanthium may be absent. Inflorescence on a culm rarely of only 1 terminal pseudanthium (*Chrysithrix*); usually inflorescence of 1 or more pseudospikelets each made up of (1-)2- many pseudanthia racemosely arranged on a rachis. Tribes Mapanieae, Syntrinemeae, Micropapyreae.

After this study of branching patterns of the ultimate units of the inflorescence, I find that there are still three problems to be resolved in the Cyperaceae as a whole.

1. Are the structures which appear to be simple bisexual flowers really true flowers or are they pseudanthia (synanthia)?

2. Are the apparently terminal female flowers really terminal or are they lateral (pseudoterminal)?

3. Are the apparent rachillas (lacking recognizable prophylls along their length) monopodial (true rachillas) or sympodial (pseudorachillas)?

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